11-16-2010 12:00 AM

Stopover biology of migratory landbirds in a heavily urbanized landscape, the New York metropolitan area

Chad L. Seewagen
The University of Western Ontario

Supervisor
Christopher Guglielmo
The University of Western Ontario

Graduate Program in Biology
A thesis submitted in partial fulfillment of the requirements for the degree in Doctor of Philosophy

STOPOVER BIOLOGY OF MIGRATORY LANDBIRDS IN A HEAVILY URBANIZED LANDSCAPE: THE NEW YORK METROPOLITAN AREA

(Spine title: Landbird stopover biology in an urban landscape)

(Thesis format: Integrated-Article)

by

Chad Lansing Seewagen

Graduate Program in Biology

A thesis submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy

The School of Graduate and Postdoctoral Studies
The University of Western Ontario
London, Ontario, Canada

THE UNIVERSITY OF WESTERN ONTARIO
SCHOOL OF GRADUATE AND POSTDOCTORAL STUDIES

CERTIFICATE OF EXAMINATION

Supervisor	Examiners
Dr. Christopher Guglielmo	Dr. Charles Trick
	Dr. Liana Zanette
	Dr. Ian Colquhoun
	Dr. Paul Rodewald

The thesis by

Chad Lansing Seewagen

entitled:

Stopover biology of migratory landbirds in a heavily urbanized landscape, the New York metropolitan area

is accepted in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

Date Nov. 16, 2010

Chair of the Thesis Examination Board

ABSTRACT

Migration routes of many Nearctic-Neotropical landbirds pass through the most urbanized regions of North America. Migrants use urban habitat fragments as stopover sites and commonly occur in cities at exceptional density. Yet, knowledge of migrant stopover biology and refueling opportunities in such places is severely limited. This dissertation examined several aspects of migrant stopover biology in the New York metropolitan area to gain a more holistic understanding of how migratory landbirds utilize urban stopover sites, and ultimately to assess the quality of urban habitats as stopover sites. I first generated morphometric predictive models using salvaged bird specimens to allow me in subsequent studies to noninvasively measure the energetic condition (fat mass) of migrants in New York City (NYC). Next I compared the refueling performance of migrants in NYC to that of conspecifics in less-disturbed forests outside of the city. Blood plasma metabolite profiles indicated that refueling conditions for migrants were no poorer in NYC than in the non-urban habitats. Further, migrant refueling rates were comparable to, and in some cases higher than, those reported in the literature for birds at various non-urban stopover sites. Measures of arthropod biomass suggested food abundance for insectivorous migrants was also similar within and outside NYC. I then showed that stopover refueling in NYC often involved substantial increases in lean mass. This finding carries implications for stopover habitat management practices, as migrants using these sites will require high-protein foods in addition to the lipid- and carbohydrate-rich foods that maximize fattening rates. Next, radio-telemetry data from a small pilot study provided one of the first descriptions of migrant stopover durations within a city. Stopover durations ranged 1-14 days and were negatively related to fat

mass, but not lean body mass, upon arrival. A larger-scale telemetry study revealed that migrant spatial behaviour in NYC was in many ways similar to what has been observed in passerine migrants in non-urban areas. Movement patterns were indicative of an ability to search for, locate, and occupy suitable microhabitat, and temporary home ranges suggested forest size was more than sufficient to meet their area requirements. Collectively, these studies provide a comprehensive assessment of the quality of urban habitats as migratory bird stopover sites. Findings indicated that the sites examined are functioning in the same fashion as less-disturbed, larger forest tracts elsewhere. No evidence was found to suggest that stopover refueling conditions within one of the world's most urbanized landscapes are inadequate for migrating landbirds.

KEYWORDS: Urban habitat, stopover site quality, refueling rate, plasma metabolites, fat mass, lean mass, spatial behaviour, stopover duration

CO-AUTHORSHIP STATEMENT

A version of Chapter III was submitted to *The Condor* with Christine Sheppard, Eric Slayton, and Christopher Guglielmo as coauthors. Dr. Sheppard assisted with logistical support and study design, and obtained a portion of the funding required for the project. Mr. Slayton supervised field crews and assisted with data collection. Dr. Guglielmo assisted with study design, provided laboratory training, obtained a portion of the project's funding, and provided editorial comments on the manuscript submitted for publication.

A version of Chapter IV has been accepted for publication by the *Journal of Comparative Physiology B* with Christopher Guglielmo as a coauthor. Dr. Guglielmo assisted with study design, approaches to data analyses, and interpretation of the study's findings. Dr. Guglielmo provided the equipment used in the study and provided editorial comments on the manuscript submitted for publication.

A version of Chapter V was published in the *Wilson Journal of Ornithology* with Christopher Guglielmo as a coauthor. Dr. Guglielmo offered interpretations of the study's findings, provided the equipment used in the study, and provided editorial comments on the manuscript.

A version of Chapter VI was published in *Acta Oecologica* with Eric Slayton and Christopher Guglielmo as coauthors. Mr. Slayton supervised field crews and co-

coordinated data collection. Dr. Guglielmo provided some of the equipment used in the study and editorial comments on the manuscript.

Dedicated to Dr. Christine Sheppard for believing in me and providing the guidance, unwavering support, and opportunities I needed to make it to where I am today. I thank you from the bottom of my heart.

ACKNOWLEDGEMENTS

I first and foremost thank my parents, Butch and Wendy, my aunt Barbara and uncle Dennis, and my grandmothers Joan and Clella for their unconditional love and support, and the frequent reminders of how proud of me they are. Their encouragement and confidence in me is what kept me going whenever I began to doubt myself. I thank each of my brothers for always being there for me if I ever needed them, especially Eric, who fostered my earliest interest in birds, taught me how to capture and band birds, and played an active and instrumental role throughout my dissertation research. I could not have done it without him. I extend my love and most heartfelt gratitude to my girlfriend, Taralynn Reynolds, for putting up with my long periods of absence, making sacrifices to stand by my side, and remaining patient as I pursued my passion. You held me up and gave me the confidence and motivation to succeed. I love you.

I am deeply grateful to my advisor, Dr. Christopher Guglielmo, for his generosity, mentorship, and friendship over the years. I am lucky to have found a fellow New Yorker who, unlike many others, could relate to my bizarre mission to learn more about the spectacle of bird migration in the Big Apple. Chris struck a perfect balance as an advisor: remaining accessible and supportive whenever I needed his guidance, while giving me ample freedom and independence to solve my own problems and find my way. I also thank the other members of my advisory committee, Drs. Jack Millar and Scott MacDougall-Shackleton, for their insight, assistance, and motivational support throughout my time at Western. Fellow bird-nerds of the Guglielmo Lab, Dr. Alice Boyle, Tara Crewe, Alex Gerson, Quentin Hays, Jay MacFarlan, Stu Mackenzie, Brendan McCabe, Liam McGuire (bat nerd), Dr. Silke Nebel, Dr. Eddy Price, Beth Thurber, and

Daria Zajac provided stimulating conversations about bird biology, lots of helpful suggestions and advice, and most importantly, plenty of fun and laughter. I would not have wanted to take this trip with a different group of people.

I can never thank the Wildlife Conservation Society (WCS) enough for its support of my research. Ornithology curators Drs. Christine Sheppard and Nancy Clum went to bat for me time and time again to make sure I had whatever I needed to accomplish my goals. Their mentorship and loyalty will have a long-lasting influence on who I am as a person and as a scientist. Countless other WCS colleagues deserve mention for their important contributions to my work, including: Marcia Arland, Patti Cooper, Dr. Peter Clyne, Lisa Eidlin, Mary Evans, Kim Fisher, Lisa Hickey, Mark Hofling, Mary Iorizzo, Danielle LaBruna, Robert Olley, Yvetta Pokorny, Dr. Eric Sanderson, and Brian Tierney.

Financial support was provided by WCS, NYC Audubon, Westchester Department of Parks, Recreation, and Conservation, and grants to C. Guglielmo from the Canadian Foundation for Innovation, Ontario Ministry of Research and Innovation, and the Natural Sciences and Engineering Research Council of Canada. Much of my research was undertaken as an Environmental Benefit Project funded through the resolution of an enforcement action for violations of the Environmental Conservation Law of New York State and its implementing regulations.

I am indebted to the many people who accommodated my needs in New York City's and Westchester County's parks. Peter Dorosh, John Jordan, and Anne Wong of the Prospect Park Alliance and Brenda Bates, Alison Beall, Beth Herr, and Rick Rogers of the Westchester County Department of Parks, Recreation, and Conservation were of outstanding assistance and never failed to make whatever logistical arrangements I

needed, often on short notice. My research required a small army of motivated, skilled field and laboratory assistants, and the hard work of the following individuals is what made each endeavor a success: Carlo Acuna, Mike Akresh, Rebecca Allmond, Brian Biefelt, Abe Borker, Katy Bruch, Rafael Campos, Oriana Chan, Courtney Clark, Kelly Colegrove, Elizabeth Corliss, Ilma Dancourt, Steve Epting, Brehan Furfey, Tim Guida, Robert Haupt, Quentin Hays, Coby Klein, Tanya Johnston, Teresa Perez, Caroline Poli, EJ Raynor, Brendan Reid, Jessie Rositano, Mark Sandfoss, Anna Scesney, Matt Sileo, Dr. Bruce Snyder, Ellen Trimarco, Emily Vaughn, and John Warzybok. I thank you all.

CONTENTS

Title Page……..……i

Certificate of Examination……...……ii

Abstract and Keywords……..iii

Co-authorship Statement……..v

Acknowledgements……..viii

Table of Contents……xi

List of Tables……xvi

List of Figures……..xvii

List of Appendices……..xviii

Chapter I: Passerine migration and the use of urban habitats as stopover sites: knowledge gaps and research objectives.

Introduction…….1

Research objectives…….4

Literature cited…….9

Chapter II: Condition indices and predictive models for noninvasive estimates of lipid mass of migrating landbirds.

Introduction……...15

Methods……..16

Study specimens……...16

Laboratory procedures……..…..17

Statistical analyses……...18

Results……19

Discussion……..21

Literature cited……..25

Tables.....……..……29

Chapter III: Stopover refueling performance of migratory landbirds in the New York metropolitan area.

Introduction……33

Methods……..37

Study sites…….37

Study species……42

Bird capture and blood sampling……43

Plasma metabolite analyses……...……..44

Food abundance……...44

Statistical analyses……...45

Results……47

Relative migrant abundance……..……..47

Hourly mass change…….47

Plasma metabolites……..…49

Food abundance……...53

Discussion……..56

Literature cited……..61

Tables……..……..…….70

Chapter IV: Use of quantitative magnetic resonance analysis and a morphometric predictive model to investigate lean body mass changes in Nearctic-Neotropical passerines at an urban stopover site.

Introduction…….……...76

Methods……..…80

Study sites…….80

Data collection……..……...80

Study species……81

Data analyses…..……..82

Results……84

Fat and lean mass contributions to total mass variation…….85

Hourly mass changes…….……..85

Recaptured birds…….86

Discussion…….86

Conclusion……89

Literature cited…….91

Tables……...……98

Chapter V: Effects of fat and lean body mass on landbird stopover durations in an urban habitat: a pilot study.

Introduction……101

Methods……103

Study site and data collection……..…….103

Radiotelemetry……..…….104

Statistical analyses…….105

Results……..106

Discussion……...…….108

Literature cited…….111

Tables……...…….…….....……115

Chapter VI: Spatiotemporal behaviours of passerine migrants at an urban stopover site: movement patterns, stopover durations, and the influence of arrival condition.

Introduction……..116

Methods……118

Study species……..118

Study site……..…….119

Capture and radio-tagging……..……..121

Radio tracking……122

Movement characteristics and home range estimation…….123

Statistical analyses…….125

Results……..126

Spring…….126

Autumn……..…….129

Discussion……130

Movement patterns…….130

Stopover duration……...133

Home range……..……..133

Influence of arrival condition……..……..134

Conclusion……..…….136

Literature cited…….…….138

Tables…….……..147

Chapter VII: Chapter summaries and concluding remarks.

Research summary……...148

Concluding remarks…….153

Literature cited…….157

Appendices

A1) Ethics committee approvals……..160

A2) Permits……..163

A3) Copyright releases……166

Vita……..…….169

LIST OF TABLES

Table 2.1. Body composition of salvaged specimens used to generate predictive lipid mass models……...29

Table 2.2. Correlations of extracted lipid mass with predictor variables……..30

Table 2.3. Partial correlation coefficients of lipid mass with condition indices……31

Table 2.4. Coefficients of determination, absolute error, and relative error of predictive models……32

Table 3.1. Differences in migratory bird capture totals among study sites……...70

Table 3.2. Hourly mass change rates of migratory birds…….……..71

Table 3.3. Mean plasma TRIG and BUTY concentrations at each study site…..…….72

Table 3.4. Variables explaining significant variation in plasma metabolite concentrations……74

Table 3.5. Relative abundance of arthropod taxonomic orders in leaf litter……..75

Table 4.1. Body composition of spring and autumn migratory birds……98

Table 4.2. Changes in fat and lean body mass per gram of total body mass…….99

Table 4.3. Net changes in total body mass, fat mass, and lean body mass of four recaptured migrants…….100

Table 5.1. Body composition and stopover duration of radio-tracked migrants…….115

Table 6.1. Fat mass, stopover duration, and home range size of ovenbirds in Prospect Park……..147

LIST OF FIGURES

Figure 2.1. Body fat percentages corresponding with subcutaneous fat scores……20

Figure 3.1. Map of canopy cover and study site locations in the New York metropolitan area……38

Figure 3.2. Migrant capture rates at each study site……..48

Figure 3.3. Spring TRIG and BUTY concentrations of ovenbirds at each study site……51

Figure 3.4. TRIG and BUTY concentrations of autumn migrants at each study site……52

Figure 3.5. Spring arthropod biomass at each study site……...54

Figure 3.6. Autumn arthropod biomass at each study site…….55

Figure 5.1. Relationship between arrival fat mass and stopover duration in Bronx Park……..107

Figure 6.1. Map of natural areas > 100 ha remaining in NYC……120

Figure 6.2. Daily changes in ovenbird movement parameters during stopovers in Prospect Park……..128

LIST OF APPENDICES

Appendix 1: Ethics committee approvals……161

Appendix 2: Permits……....164

Appendix 3: Copyright releases……...?

CHAPTER I

PASSERINE MIGRATION AND THE USE OF URBAN HABITATS AS STOPOVER SITES: KNOWLEDGE GAPS AND RESEARCH OBJECTIVES

INTRODUCTION

Each phase of a migratory bird's life cycle presents its own challenges; yet neither reproduction nor overwintering periods are perhaps as demanding and carry as great of a risk of mortality as migration (Sillett and Holmes 2002). Nesting and wintering grounds of passerine migrants are often separated by thousands of kilometers and successful movements from one area to the other are complicated by unpredictable and changing weather, food availability, competition, and predation risk experienced *en route* (Moore et al.1995). Unlike the breeding and winter seasons, migration requires birds to continuously exploit potentially novel and unfamiliar habitats at stopover points along the way to recover expended energy stores. Substantially more time and energy is spent during stopovers than during flight (Wikelski et al. 2003, Bowlin et al. 2005) and thus the conditions experienced at stopover sites largely determine the economy, duration, and success of migration (Moore et al. 2003). Migration performance not only affects survival during migration, but may also indirectly affect success in subsequent phases of the life cycle, which can together limit bird populations (Butler 2000, Sillett and Holmes 2002, Smith and Moore 2003, Newton 2006).

Stopover site selection processes are poorly understood (Petit 2000), but migrants are expected to utilize habitats that allow them to refuel most efficiently and remain close to their migratory schedules while avoiding predation (Lindström and Alerstam 1992).

Upon landfall, migrants typically explore a new stopover site widely to obtain information about predation, competition, and resource distribution, and then either depart that night or select a microsite to occupy for additional days of rest and refueling (Chernetsov 2005, Chernetsov and Mukhin 2006, Paxton et al. 2008, Chapter VI). Stopover durations of passerines are highly variable, often lasting only one day but sometimes lasting more than a week (e.g., Morris et al. 1996, Tsvey et al. 2007, Chapters V and VI). Stopover duration can be influenced by numerous factors including weather, predation risk, competition, and distance to final destination (Yong and Moore 1997, Åkesson and Hedenström 2000, Dierschke and Delingat 2001, Hays 2008). Arrival condition and refueling ability at the stopover site can also be primary determinants of how long birds remain at a stopover site (Loria and Moore 1990, Schaub et al. 2008, Matthews and Rodewald 2010a). Passerines typically migrate with fat stores that represent 10-50% of total body mass (Child 1969, Spengler et al. 1995, Seewagen 2008), and during hyperphagic stopover refueling birds can replace mass lost in flight by as much as 5% of their total body mass per day (Bonter et al. 2007, Seewagen and Slayton 2008). Often stopover refueling includes the deposition of both fat and lean mass (Karasov and Pinshow 1998, Wirestam et al. 2008, Chapter IV).

Sufficient refueling opportunities, and ultimately the ability to successfully travel between nesting and wintering grounds is dependent on an availability of quality stopover habitat (Moore et al. 1995). Widespread habitat loss and fragmentation throughout North America has reduced the amount of stopover habitat available to Nearctic-Neotropical migrants and has likely contributed to recent population declines of several species (Kirby et al. 2008, Carlisle et al. 2009). Identification and preservation of important

stopover habitat has become an integral component of migratory bird conservation strategies (McCann et al. 1993, Mehlman et al. 2005, Kirby et al. 2008), but such efforts have been hampered by an incomplete understanding of migrant ecology and behaviour during stopovers, and how to best assess stopover habitat quality (Petit 2000, Mehlman et al. 2005, Carlisle et al. 2009).

Much of the habitat loss, fragmentation, and degradation in the U.S. is attributable to urbanization and urban sprawl (McKinney 2002). The largest metropolitan areas in the U.S. are concentrated along North America's coasts, as are the migration paths of many Nearctic-Neotropical migratory landbird species. Concentrations of passage migrants routinely occur in many cities as a result. Although this phenomenon has been well-documented and brought several city parks recognition as premier bird-watching locations (Fowle and Kerlinger 2001, Milne 2007), it remains almost entirely unknown whether these habitats within heavily urbanized landscapes can serve as adequate stopover sites for migrants. The presence of large numbers of migrants at an urban stopover site cannot be taken to indicate high quality habitat, as it may simply reflect a lack of nearby alternatives.

Urban forests are typically small in size and highly fragmented and isolated. They are characterized by abundant invasive plants and animals, large levels of human disturbance, multiple forms of pollution, and management practices that emphasize aesthetic appearance and recreational usage. It follows that urban areas support relatively low levels of biodiversity (Czech et al. 2000; McKinney 2002, 2006) and are unexpected to provide high quality stopover habitat for migratory birds (Mehlman et al. 2005). However, two recent studies of migrant refueling rates in North American cities have

indicated that urban forests can in fact be suitable stopover sites (Seewagen and Slayton 2008, Craves 2009). Seewagen and Slayton (2008) and Craves (2009) found that multiple species of landbird migrants were able to gain significant body mass during stopovers within New York City and Dearborn, Michigan, respectively. A recent study of Swainson's thrush (*Catharus ustulatus*) movement patterns in the city of Columbus, Ohio also suggested urban habitats met the stopover needs of this migrant landbird (Matthews and Rodewald 2010b). Although these studies demonstrate that urban habitats have the potential to be suitable stopover sites, generalization of their findings elsewhere is limited by variation in habitat characteristics such as forest size, vegetation composition, predators, food availability, and levels of human disturbance, that likely affect stopover site quality.

RESEARCH OVERVIEW

The objective of my dissertation research was to comprehensively assess the quality of urban stopover sites by studying multiple aspects of migratory songbird stopover biology in and around New York City (NYC), the United States' largest city. Advancing our currently limited understanding of migrant behaviour, ecology, and refueling physiology in urban stopover sites is a necessary antecedent to science-based decision-making about habitat conservation, restoration, and management for migrating birds in metropolitan areas.

In Chapter II, I use salvaged bird specimens to generate morphometric predictive models that allow me in subsequent chapters to noninvasively measure the energetic condition (fat mass) of living migrants captured in NYC. I also evaluate the performance

of some common migratory bird condition indices such as visible subcutaneous fat scores (Dunn 2003). Measurement of fat is central to the study of migration physiology and ecology, yet the abilities of the most widely used non-lethal techniques to predict true fat content are seldom validated. I use the predictive model for the ovenbird (*Seiurus aurocapillus*) developed in this chapter to examine in Chapter IV what proportion of total body mass changes during stopovers in NYC is attributable to fat versus lean tissue in this species. I use the model again in Chapter VI to examine the influence of arrival fat stores on ovenbird stopover durations, movement patterns, and temporary home range sizes.

In Chapter III, I assess the refueling conditions provided by three NYC parks that are well-known for their use as stopover sites by migrating birds. Migrant refueling rate is the most common measure of stopover habitat quality (Dunn 2000, Guglielmo et al. 2005) and this chapter serves as the centerpiece of my dissertation. I use plasma metabolites to indicate rates of mass change (Jenni-Eiermann and Jenni 1994, Guglielmo et al. 2005) and compare the refueling performances of multiple species in NYC to those of conspecifics in two less-disturbed, non-urban forests outside of the city. Because plasma metabolites only provide a relative measure of refueling, I use regressions of body mass and capture time to also obtain quantitative estimates of the actual mass change rates of migrants in NYC (e.g., Winker et al. 1992, Morris et al. 1996, Carlisle et al. 2005). In this chapter I also measure leaf litter arthropod biomass within and outside NYC to assess food availability for ground-foraging, insectivorous migrants such as ovenbirds and thrushes.

In Chapter IV, I more closely examine migrant refueling in NYC to determine whether lean tissues contribute to total body mass gains. Fat is the primary fuel used by birds during migration (McWilliams et al. 2004), and it was at one time believed that fat was the only tissue to change in mass (Odum et al. 1964). More recently it has become clear that lean body mass is not homeostatic, but instead fluctuates considerably prior to and throughout migration (Lindström and Piersma 1993, Karasov and Pinshow 1998, Bauchinger et al. 2005). Most studies of lean mass dynamics in free-living birds, however, have focused on long-distance migrant shorebirds or Old World passerines at major geographical barriers where they are challenged to make the longest non-stop flight of their migration. Much less is known about lean mass changes in Nearctic-Neotropical passerine species, or in passerines when stopover habitat is more continuously available and shorter flights are possible (Åkesson et al. 1992, Bauchinger and Biebach 2005). The role of lean mass in stopover refueling has also yet to be examined in an urban system. In this chapter I use either quantitative magnetic resonance (QMR) analysis or a predictive model generated in Chapter II to measure body composition and investigate lean mass variation among four Nearctic-Neotropical passerine species at two NYC stopover sites. Understanding the extent to which lean tissues are involved in stopover refueling is important for identifying the most important nutrient sources that stopover habitats must provide (Karasov and Pinshow 1998).

In Chapter V, I analyze data from a pilot study I conducted to test the feasibility of radio tracking birds in an urban setting before proceeding with the larger scale telemetry study planned for following seasons (Chapter VI). This pilot study was concurrent with the QMR body composition analyses conducted in Chapter IV. The

stopover duration and fat and lean body mass data obtained by radio-telemetry and QMR, respectively, afforded an additional opportunity to examine the relationships among these variables. I coupled telemetry and QMR data from the eleven migrants used in the pilot study to examine whether arrival fat and lean body mass affected their stopover durations. Many studies have shown that arrival fat mass can strongly determine the amount of time birds remain at a stopover site (e.g., Cherry 1982, Yong and Moore 1997, Mathews and Rodewald 2010b), but I am unaware of any previous investigation of the influence of lean body mass on migrant stopover duration. This chapter presents some of the first data on the stopover durations of migratory birds in a major urban center like NYC.

In Chapter VI, I examine the movement patterns, temporary home range sizes, and stopover durations of ovenbirds radio-tracked in Prospect Park, NYC. I use a predictive model from Chapter II to determine whether arrival fat stores influence any of these metrics. Several recent studies in non-urban areas have shown landbird migrant behaviour to involve exploratory, linear movements upon arrival at a new stopover site, followed by more clustered movements on subsequent days presumably after suitable microhabitat has been located (Chernetsov 2005, Chernetsov and Mukhin 2006, Paxton et al. 2008). It is unknown whether migrants in urban stopover sites exhibit this same "search and settling" behaviour that is characteristic of birds in non-urban settings. If habitat quality is low and levels of disturbance are high, birds may continuously move throughout the stopover site without ever settling, and depart when temporal and energetic costs of the stopover outweigh the benefits. This chapter presents some of the first detailed information on the spatial behaviour of landbird migrants at an urban

stopover site (see also Matthews and Rodewald 2010b). Knowledge of migrant habitat use and stopover behaviours is considered necessary for effective stopover site management in both rural and urban areas alike (Petit 2000, Mehlman et al. 2005, Chernetsov 2006, Pennington et al. 2008).

Taken together, these studies are intended to provide a holistic understanding of how migratory landbirds utilize urban habitats as stopover sites, the quality of urban habitats as stopover sites, and ultimately how to manage habitats in cities for migrating birds. Urban habitats seem largely overlooked in migratory bird conservation planning, possibly because of their inability to support large populations of breeding birds. Yet areas that are unsuitable for breeding may still function as valuable stopover habitat (Pennington et al. 2008). By serving as stopover sites, I argue that habitat fragments within cities that otherwise may be of limited significance to wildlife have the potential to be of great importance to migrating birds and help facilitate movements of populations on regional and continental scales. Without further study, however, it will remain largely unknown whether urban stopover sites are filling this role.

LITERATURE CITED

Åkesson S, Karlsson L, Pettersson J (1992) Body composition and migration strategies: a comparison between robins (*Erithacus rubecula*) from two stop-over sites in Sweden. Vogelwarte 36:188-195.

Åkesson S, Hedenström A (2000) Wind selectivity of migratory flight departures in birds. Behavioral Ecology and Sociobiology 47:140-144.

Bauchinger U, Biebach H (2005) Phenotypic flexibility of skeletal muscles during long distance migration of garden warblers: muscle changes are differentially related to body mass. Annals of the New York Academy of Sciences 1046:271-281.

Bauchinger U, Wohlmann A, Biebach H (2005) Flexible remodeling of organ size during spring migration of the garden warbler (Sylvia borin). Zoology 108:97-106.

Bonter DN, Donovan TM, Brooks EW (2007) Daily mass changes in landbirds during migration stopover on the south shore of Lake Ontario. Auk 124:122-133.

Bowlin MS, Cochran WW, Wikelski MC (2005) Biotelemetry of New World thrushes during migration: physiology, energetics and orientation in the wild. Integrative and Comparative Biology 45:295-304.

Butler RW (2000) Stormy seas for some North American songbirds: Are declines related to severe storms during migration? Auk 117:518-522.

Carlisle JD, Kaltenecker GS, Swanson DL (2005) Stopover ecology of autumn landbird migrants in the Boise foothills of southwestern Idaho. Condor 107:244-258.

Carlisle JD, Skaken SK, Kus BE, van Riper III C, Paxton KL, Kelly JF (2009) Landbird migration in the American West: recent progress and future research directions. Condor 111:211-225.

Chernetsov N (2005) Spatial behavior of medium and long-distance migrants at stopovers studied by radio tracking. Annals of the New York Academy of Sciences 1046: 242-252.

Chernetsov N (2006) Habitat selection by nocturnal passerine migrants en route: mechanisms and results. Journal of Ornithology 147:185-191.

Chernetsov N, Mukhin A (2006) Spatial behavior of European Robins during migratory stopovers: a telemetry study. Wilson Bulletin 118:364-373.

Cherry JD (1982) Fat deposition and length of stopover of migrant white-crowned sparrows. Auk 99:725-732.

Child GI (1969) A study of non-fat weights in migrating Swainson's thrushes (*Hylocichla ustulata*). Auk 86:327-338.

Craves JA (2009) A fifteen year study of fall stopover patterns of *Catharus* thrushes at an inland, urban site. Wilson Journal of Ornithology 121:112-118.

Czech B, Krausman PR, Devers PK (2000) Economic associations among causes of species endangerment in the United States. BioScience 50:593-601.

Dierschke V, Delingat J (2001) Stopover behaviour and departure decision of Northern Wheatears, *Oenanthe oenanthe*, facing different onward non-stop flight distances. Behavioral Ecology and Sociobiology 50:535-545.

Dunn EH (2000) Temporal and spatial patterns in daily mass gain of Magnolia Warblers during migratory stopover. Auk 117:12-21.

Dunn EH (2003) Recommendations for fat scoring. North American Bird Bander 28:58-63.

Fowle M, Kerlinger P (2001) The New York City Audubon Society guide to finding

birds in the metropolitan area. Cornell University Press, New York.

Guglielmo CG, Cerasale DJ, Eldermire C (2005) A field validation of plasma metabolite profiling to assess refueling performance of migratory birds. Physiological and Biochemical Zoology 78:116-125.

Hays QR (2008) Stopover behavior and refueling physiology in relation to migration distance in Wilson's Warblers (*Wilsonia pusilla*). Thesis. University of Western Ontario, London, Ontario, Canada.

Jenni-Eiermann S, Jenni L (1994) Plasma metabolite levels predict individual body mass changes in a small long-distance migrant, the garden warbler. Auk 111:888-899.

Karasov WH, Pinshow B (1998) Changes in lean mass and in organs of nutrient assimilation in a long-distance passerine migrant at a springtime stopover site. Physiological Zoology 71:435-448.

Kirby JS, Stattersfield AJ, Butchart SHM, Evans MI, Grimmett RFA, Jones VR, O'Sullivan J, Tucker GM, Newton I (2008) Key conservation issues for migratory land- and waterbird species on the world's major flyways. Bird Conservation International 18:49-73.

Lindström Å, Alerstam T (1992) Optimal fat loads in migrating birds: A test of the time minimization hypothesis. American Naturalist 140:477-491.

Lindström Å, Piersma T (1993) Mass changes in migrating birds: the evidence for fat and protein storage re-examined. Ibis 135:70-87.

Loria DE, Moore FR (1990) Energy demands of migration on Red-eyed Vireos, *Vireo olivaceus*. Behavioral Ecology 1:24-35.

Matthews S, Rodewald P (2010a) Urban forest patches and stopover duration of migratory Swainson's thrushes. Condor 112:96-104.

Matthews S, Rodewald P (2010b) Movement behaviour of a forest songbird in an urbanized landscape: the relative importance of patch-level effects and body condition during migratory stopover. Landscape Ecology 25:955-965.

McCann JM, Mabey SE, Niles LJ, Bartlett C, Kerlinger P (1993) A regional study of coastal migratory stopover habitat for neotropical migrant songbirds: land management implications. Transactions of the North American Wildlife and Natural Resources Conference 58:398-407.

McKinney ML (2002) Urbanization, biodiversity, and conservation. BioScience 52:883 890.

McKinney ML (2006) Urbanization as a major cause of biotic homogenization. Biological Conservation 127:247-260.

McWilliams SR, Guglielmo C, Pierce B, Klaassen M (2004) Flying, fasting, and feeding in birds during migration: a nutritional and physiological ecology perspective. J Avian Biology 35:377-393.

Mehlman DW, Mabey SE, Ewert DN, Duncan C, Abel B, Cimprich D, Sutter RD, Woodrey MS (2005) Conserving stopover sites for forest-dwelling migratory landbirds. Auk 122:1281-1290.

Milne P (2007) Where to watch birds in world cities. Yale University Press, New Haven.

Moore F, Mabey S, Woodrey M (2003) Priority access to food in migratory birds: age, sex, and motivational asymmetries. Pp 281-292 in: Avian migration (Berthold P, Gwinner E, Sonnenschein E, eds). Springer-Verlag, Berlin.

Moore FR, Gauthreaux SA, Kerlinger P, Simons TR (1995) Habitat requirements during migration: important link in conservation. Pp 121-144 in: Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues (Martin TE, Finch DM, eds). Oxford University Press, New York.

Morris SR, Holmes DW, Richmond ME (1996) A ten year study of the stopover patterns of migratory passerines during fall migration on Appledore Island, Maine. Condor 98:395-408.

Newton I (2006) Can conditions experienced during migration limit the population levels of birds? Journal of Ornithology 147:146-166.

Odum EP, Rogers DT, Hicks DL (1964) Homeostasis of nonfat components of migrating birds. Science 143:1037-1039.

Paxton KL, Van Riper III C, O'Brien C (2008) Movement patterns and stopover ecology of Wilson's warblers during spring migration on the lower Colorado River in southwestern Arizona. Condor 110:672-681.

Pennington DN, Hansel J, Blair RB (2008) The conservation value of urban riparian areas for landbirds during spring migration: Land cover, scale, and vegetation effects. Biological Conservation 141:1235-1248.

Petit DR (2000) Habitat use by landbirds along Neartic-Neotropical migration routes: Implications for conservation of stopover habitats. Studies in Avian Biology 20: 15-33.

Schaub M, Jenni L, Bairlein F (2008) Fuel stores, fuel accumulation, and the decision to depart from a migration stopover site. Behavioral Ecology 19:657-666.

Seewagen CL (2008) Lipid content of Nearctic-Neotropical migratory passerines killed

during stopovers in a New York City park. Northeastern Naturalist 15:87-96.

Seewagen CL, Slayton EJ (2008) Mass changes of migratory landbirds during stopovers in a New York City park. Wilson Journal of Ornithology 120:296-303.

Sillett TS, Holmes RT (2002) Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296–308.

Smith RJ, Moore FR (2003) Arrival fat and reproductive performance in a long-distance passerine migrant. Oecologia 134:325-331.

Spengler TJ, LeBerg PL, Barrow Jr WC (1995) Comparison of condition indices in migratory passerines at a stopover site in coastal Louisiana. Condor 97:438-444.

Tsvey A, Bulyuk VN, Kosarev V (2007) Influence of body condition and weather on departures of first-year European Robins, *Erithacus rubecula*, from an autumn migratory stopover site. Behavioral Ecology and Sociobiology 61:1665-1674.

Wikelski M, Tarlow EM, Raim A, Diehl RH, Larkin RP, Visser GH (2003) Costs of migration in free-flying songbirds. Nature 423:704.

Winker K, Warner DW, Weisbrod AR (1992) Daily mass gains among woodland migrants at an inland stopover site. Auk 109:853-862.

Wirestam R, Fagerlund T, Rosèn M, Hedenström A (2008) Magnetic resonance imaging for noninvasive analysis of fat storage in migratory birds. Auk 125:965-971

Yong W, Moore FR (1997) Spring stopover of intercontinental migratory thrushes along the northern coast of the Gulf of Mexico. Auk 114:263-278.

CHAPTER II

CONDITION INDICES AND PREDICTIVE MODELS FOR NONINVASIVE ESTIMATES OF LIPID MASS OF MIGRATING LANDBIRDS[1]

INTRODUCTION

Fat is the primary source of fuel for the energy-demanding flights of migrating birds (Blem 1990), and the ability of birds to store fat throughout migration is a chief determinant of their overall migration success (Moore et al. 1995). As such, measurement of fat is central to the study of avian migration ecology. The quantity of fat in breeding and wintering birds is often of interest because lipid storage can affect reproduction and survival during these life history stages (Lima 1986, Rogers 1987, Rowe et al. 1994). Body condition attained during one season can also affect fitness and survival during subsequent seasons (Smith and Moore 2003, Studds and Marra 2005).

Lipid mass can be measured via solvent extraction of dead specimens. This method offers accurate direct measurements, but is time-consuming, costly, and requires sacrificing birds or acquiring birds that have already died from other causes. Noninvasive alternative methods are less accurate than chemical extraction, but are advantageous because they allow repeated measurements on the same individuals and can be used on species of conservation concern that cannot be sacrificed. Additionally, many noninvasive methods are inexpensive and can be used quickly and easily in the field (Krementz and Pendleton 1990, Roby 1991, Rogers 1991, Burger 1997).

[1] A version of this chapter has been published (Seewagen 2008) and is presented here with permission from John Wiley & Sons, Inc.

Modern noninvasive techniques of measuring fat content, such as magnetic resonance analysis, dual-energy x-ray absorptiometry (DXA), and heavy water dilution (Karasov and Pinshow 1998, Piersma and Klaassen 1999, Korine et al. 2004), are accurate, but remain cost-prohibitive to many. Popular inexpensive noninvasive methods include visible subcutaneous fat scores (Moore and Kerlinger 1987, Dunn 2003), body mass (Jones et al. 2002), body mass corrected for structural size variation (Johnson et al. 1985, Winker 1995, Benson and Winker 2005), and predictive regression models built from live birds with no visible subcutaneous fat (Strong and Sherry 2000).

Some studies have validated the ability of these latter methods to predict true fat content in passerines (e.g., Rogers 1991, Conway et al. 1994, Spengler et al. 1995). Method performance, however, may vary considerably among species, and species-specific models are needed to obtain accurate estimates of lipid mass (Skagen et al. 1993, Spengler et al. 1995). I examined relationships between three routinely used indicators of fat content and actual lipid mass to construct predictive equations and determine techniques that best estimate fat content in three passerine migrants that I expected to be among the focal species in subsequent chapters: Swainson's thrush (*Catharus ustulatus*), common yellowthroat (*Geothlypis trichas*), and ovenbird (*Seiurus aurocapillus*).

METHODS

Study specimens

The birds used in this study were killed by building collisions during spring and autumn migrations through New York, New York, and Toronto, Ontario in 2005-2006. Specimens were salvaged by the Fatal Light Awareness Program (FLAP) and New York

City Audubon Society (NYCAS) to document the hazards of illuminated skyscrapers and reflective windows to migrants (Knoepfli and Krajnc 2005, Gelb and Delecretaz 2006). Due to the manner of specimen collection, the exact time elapsed between death and collection was unknown, but was estimated to be no longer than six hours (FLAP, NYCAS pers. comm.). Birds were bagged and stored frozen at -20° C for up to six months before processing.

Laboratory procedures

Specimens were thawed at room temperature until flexible. Unflattened wing chord was measured to the nearest 1 mm. Visible subcutaneous fat in the furcular hollow was ranked on a 6-point scale (Moore and Kerlinger 1987), with the carcass positioned as a living bird would be positioned during fat scoring. The appearance of the fat was not noticeably different from that of living birds and I assumed scoring performance was unaffected by the birds' state (i.e., dead vs. alive; Krementz and Pendleton 1990). Birds were weighed to the nearest 0.001 g (Denver Instrument, Denver, CO.). A ventral midline incision was made to expose the thoracic and abdominal cavities and expedite desiccation. Birds were then oven-dried to a constant mass at 75° C. Dry carcasses were re-weighed and homogenized (including feathers) with a household electric blender. Soluble fat was extracted from duplicate 1 g (± 0.1 g) samples of the homogenate using petroleum ether in a Soxtec apparatus (FOSS Inc., Laurel, MD). Following extraction, samples were oven-dried overnight and weighed the following day. Mass losses of duplicate samples were converted to percentages of original dry sample masses and

averaged (CV of all duplicates < 15%). The average value (hereafter lipid %) was multiplied by total dry body mass to yield total body lipid mass (hereafter lipid mass).

Statistical analyses

Pearson's product-moment correlations were used to measure the relationships between chemically-determined lipid mass and total wet body mass, wing chord, wet mass/wing chord, fat score, and percentage water content (wet mass – dry mass/wet mass). Multiple regression was used to generate partial correlation coefficients and re-examine the associations of lipid mass with total wet body mass, wing chord, and fat score individually while controlling the effects of the other variables (Spengler et al. 1995, Zar 1999). The initial Pearson's correlation tests found percentage water content and mass/ wing chord were highly correlated with the other predictor variables in most cases and were thus omitted from this regression analysis to avoid multicollinearity (Zar 1999).

I used stepwise multiple regression with forward selection ($\alpha = 0.1$) to determine what combination of variables best explained variation in extracted lipid mass in each species. Equations incorporating every variable and equations including only variables chosen by forward selection are presented. Following Conway et al. (1994) and Spengler et al. (1995), I evaluated the predictive ability of each equation with cross-validation tests. Coefficients of determination were calculated as total sum of squares minus predicted residual sum of squares divided by total sum of squares. Predicted residuals from multiple regression were then used to calculate the absolute error (mean of the absolute value of predicted residuals) and percent error (absolute error/true lipid mass) of each model (Conway et al. 1994).

Statistical tests were performed with SYSTAT version 10.0 (SPSS Inc., Chicago, IL) and SAS version 9.0 (SAS Institute Inc., Cary, NC). Results were considered significant at $\alpha \leq 0.05$.

RESULTS

Lipid %, mean fat score, and percentage water content were comparable across species (Table 2.1). In all three species, birds with no visible subcutaneous fat (i.e., zero fat score), on average, possessed considerable quantities of fat ranging from 9.8-19.7% of total dry body mass (Fig. 2.1).

Body mass, body mass/wing chord, fat score, and percentage water content were significantly correlated with lipid mass in all species (Table 2.2). Wing chord was not significantly correlated with lipid mass in any species, and was only significantly correlated with lean body mass for common yellowthroats ($r = 0.45$, $P = 0.01$). Only in common yellowthroats was there a stronger correlation of lipid mass with size-corrected body mass than with body mass alone. Lipid mass was correlated with percentage water content in each species more than any other variable (Table 2.2). After controlling for the effects of the other indices, body mass and fat score remained significantly correlated with lipid mass in all three species, and wing chord became significantly correlated with lipid mass in the common yellowthroat (Table 2.3).

Models that included every predictor variable accounted for 74-88% of the observed variation in lipid mass (Table 2.4). Forward-selected models explained 69-87% of lipid mass variation. For each model, the coefficients of determination calculated from cross-validation tests were lower than those originally produced by multiple regression.

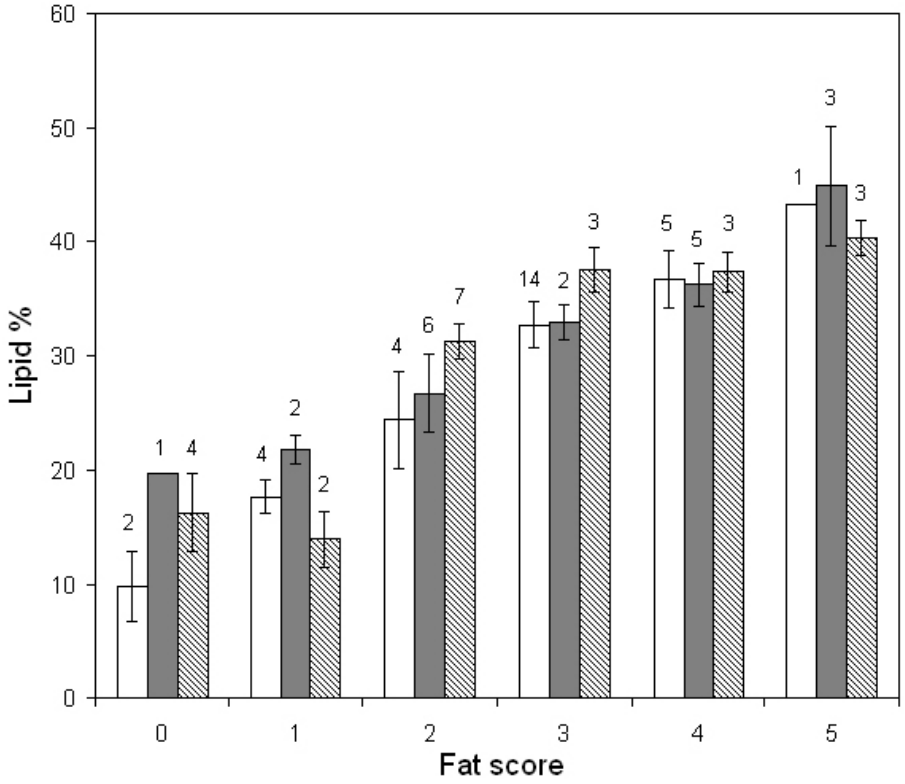

Figure 2.1. Corresponding mean (± SE) lipid % (subsample lipid mass/dry mass) of different fat scores (left to right: common yellowthroat, ovenbird, Swainson's thrush). Sample sizes above bars.

Percent errors were lowest for ovenbird and Swainson's thrush models (14.6% and 18.7%, respectively). Percent error was highest in the all-inclusive model for common yellowthroats (30.1%). Variables included by forward selection were the same for ovenbirds and Swainson's thrushes (fat score and body mass). Fat score was selected for inclusion in all three species (Table 2.4). The regression model for Swainson's thrushes presented by Spengler et al. (1995; Lipid mass = −15.184 + 0.636*Body mass + 0.679*Fat score) overestimated lipid mass of the specimens in my study by an average of 92%.

DISCUSSION

Three simple, inexpensive indices and models were identified for accurately estimating lipid mass in common yellowthroats, ovenbirds, and Swainson's thrushes. Fat score and body mass were highly correlated with total body fat in each species. Selection procedures included fat score in the predictive models for all species, and body mass was included in two of the three species. Body mass/wing chord was selected over body mass in the common yellowthroat but not the other two species. The non-significant correlations between wing chord and lean body mass may be due to variation in lean tissue mass among birds of equal structural size because fat is not the only tissue to change in mass throughout migration (Piersma 1990, Scott et al. 1994, Karasov and Pinshow 1998, Chapter V). It is also possible that wing chord is an unreliable indicator of structural size in these species (Rising and Somers 1989). Other measurements (e.g., tarsus length) could be better for adjusting body mass for body size in ovenbirds and Swainson's thrushes, but were not examined in this study.

The sizable fat loads of birds with no visible fat indicate that fat scoring provides conservative measures of energy stores. Birds scored as zero are likely to have intraperitoneal or other unseen metabolically available fat deposits (see also Rogers 1991). In turn, using the body masses of zero fat class birds to estimate lean body mass for a species (e.g., Dunn 2001, Mulvihill et al. 2004), and subsequently quantify the lipid content of conspecifics as the difference of that lean body mass and total body mass, will probably underestimate true lipid mass. The poor resolution at the lower end of the scale may also make fat scoring insufficient for studies of bird populations with limited energy stores (Rogers 1991).

Regression equation performance is better gauged by the extent of prediction error as determined by cross-validation tests than by coefficients of determination (Conway et al. 1994). Judging models here by their error showed each model to perform better than suggested by their coefficients of determination. Estimating lipid mass in the common yellowthroat, the smallest species, was least accurate, as the error represented a greater proportion of its average fat mass (27.5%) than the other larger species examined. The forward-selected model for the common yellowthroat may be too weak to detect all but gross differences in lipid mass among study groups. Conversely, the models produced for Swainson's thrushes and ovenbirds had low prediction errors and appear sufficient for estimating lipid mass of living birds with acceptable accuracy. The models are likely inadequate, however, for revealing subtle differences in lipid mass such as those of birds recaptured within the same day.

A previous model for Swainson's thrushes presented by Spengler et al. (1995) included the same variables as in my study (fat score and body mass), but had greater

prediction error (27.3%). Further, the model overestimated the lipid content of the Swainson's thrushes I examined by an average of 92%. This large error may be a product of inter-observer variation during fat scoring (Krementz and Pendleton 1990), or the drastic differences in body composition between the birds used in each study. The average lipid content (12.4%) and lean dry body mass (7.7 g) of the birds examined by Spengler et al. (1995) were considerably lower than those I examined (Table 2.1). This is likely a consequence of Spengler et al. (1995) examining birds that had just completed non-stop flights across the Gulf of Mexico, and my use of birds collected in a region without such formidable geographic barriers. Models built from one set of birds may not be able to predict lipid mass in entirely different study groups with accuracy. Season and geographic location are likely to significantly affect regression model performance (Spengler et al. 1995) and should be considered when estimating lipid mass in this manner. It should be noted that spring and autumn migrants, as well as individuals of different sex and age, were combined to obtain sufficient sample sizes when generating the models presented here. Such combinations likely weaken model accuracy, and development of models that account for potential variation within these variables is recommended.

Fat scoring was the best single indicator of lipid mass in two of the three species examined. Fat score was significantly correlated with lipid mass and was included in forward-selected models in each species. Body mass was also found to be a strong index of lipid mass. Modern noninvasive techniques for assessing body composition, such as magnetic resonance analysis and DXA require costly equipment that makes them unavailable to many researchers. Traditional simple and inexpensive approaches to

assessing lipid content such as those examined here are therefore likely to remain commonplace and useful in field studies of birds.

LITERATURE CITED

Benson AM, Winker K (2005) Fat-deposition strategies among high-latitude passerine migrants. Auk 122:544-557.

Blem CR (1990) Avian energy storage. Current Ornithology 7:59-113.

Burger MF (1997) Estimating lipid and lean masses in a wintering passerine: an evaluation of TOBEC. Auk 114:762-769.

Conway CJ, Eddleman WR, Simpson KL (1994) Evaluation of lipid indices of the Wood Thrush. Condor 96:783-790.

Dunn EH (2001) Mass change during migration stopover: a comparison of species groups and sites. Journal of Field Ornithology 72:419-432.

Dunn EH (2003) Recommendations for fat scoring. North American Bird Bander 28:58-63.

Gelb Y, Delecretaz N (2006) Avian window strike mortality at an urban office building. Kingbird 56:190-198.

Johnson DH, Krapu GL, Reinecke KJ, Jorde DG (1985) An evaluation of condition indices for birds. Journal of Wildlife Management 49:569-575.

Jones J, Francis CM, Drew M, Fuller S, Ng MWS (2002) Age related differences in body mass and rates of mass gain of passerines during autumn migratory stopover. Condor 104:49-58.

Karasov WH, Pinshow B (1998) Changes in lean mass and in organs of nutrient assimilation in a long-distance passerine migrant at a springtime stopover site. Physiological and Biochemical Zoology 71:435-448.

Knoepfli KE, Krajnc S (2005) Charting a course for bird-friendly cities. BirdWatch

Canada 33:4-6.

Korine C, Daniel S, Van Tets IG, Yosef R, Pinshow B (2004) Measuring fat mass in small birds by dual-energy x-ray absorptiometry. Physiological and Biochemical Zoology 77:522-529.

Krementz DG, Pendleton GW (1990) Fat scoring: sources of variability. Condor 92:500-507.

Lima SL (1986) Predation risk and unpredictable feeding conditions: determinants of body mass in birds. Ecology 67:377-385.

Moore FR, Kerlinger P (1987) Stopover and fat deposition by North American wood warblers following spring migration over the Gulf of Mexico. Oecologia 74:47-54.

Moore FR, Gauthreaux SA, Kerliner P, Simons TR (1995) Habitat requirements during migration: important link in conservation. Pp 121-144 in: Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues (Martin TE, Finch DM, eds.). Oxford University Press, New York.

Mulvihill RS, Leberman RC, Leppold AJ (2004) Relationships among body mass, fat, wing length, age, and sex for 170 species of birds banded at Powdermill Nature Reserve. Eastern Bird Banding Association Monograph No. 1.

Piersma T (1990) Pre-migratory “fattening” usually involves more than the deposition of fat alone. Ringing and Migration 11:113-115.

Piersma T, Klaassen M (1999) Methods of studying the functional ecology of protein and

organ dynamics in birds. Pp 36-51 in: Proceeding of the 22nd International Ornithological Congress, Durban (Adams NJ, Slotow RH, eds.). BirdLife South Africa, Johannesburg.

Rising JD, Somers KM (1987) The measurement of overall body size in birds. Auk 106:666-674.

Roby DD (1991) A comparison of two noninvasive techniques to measure total body lipid in birds. Auk 108:509-518.

Rogers CM (1987) Predation risk and fasting capacity: Do wintering birds maintain optimal body mass? Ecology 68:1051-1061.

Rogers CM (1991) An evaluation of the method of estimating body fat in birds by quantifying visible subcutaneous fat. Journal of Field Ornithology 62:349-356.

Rowe L, Ludwig D, Schluter D (1994) Time, condition, and the seasonal decline of avian clutch size. American Naturalist 143:698-722.

Scott I, Mitchell PI, Evans PR (1994) Seasonal changes in body mass, body composition and food requirements in wild migratory birds. Proceedings of the Nutrition Society 53:521-531.

Seewagen CL (2008) An evaluation of condition indices and predictive models for non-invasive estimates of lipid mass of migrating Common Yellowthroats, Ovenbirds and Swainson's Thrushes. Journal of Field Ornithology 79:80-86.

Skagen SK, Knopf FL, Cade BS (1993) Estimation of lipids and lean mass of migrating sandpipers. Condor 95:944-956.

Smith RJ, Moore FR (2003) Arrival fat and reproductive performance in a long distance passerine migrant. Oecologia 134:325-331.

Spengler TJ, LeBerg PL, Barrow WC (1995) Comparison of condition indices in migratory passerines at a stopover site in coastal Louisiana. Condor 97:438-444.

Strong AM, Sherry TW (2000) Habitat-specific effects of food abundance on the condition of ovenbirds wintering in Jamaica. Journal of Animal Ecology 69:883-895.

Studds CE, Marra PP (2005) Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. Ecology 86:2380-2385.

Winker K (1995) Autumn stopover on the Isthmus of Tehuantepec by woodland Nearctic-Neotropic migrants. Auk 112:690-700.

Zar JH (1999) Biostatistical analysis, 4th ed. Prentice Hall, Englewood Cliffs.

Table 2.1. Mean (± SD) values of wet mass, lean mass, lean dry mass, lipid mass, lipid percentage (subsample lipid mass/dry mass), wing chord, fat score, and water percentage of three species of passerine killed by building collisions during spring and autumn migration in New York, New York and Toronto, Ontario, 2005-2006.

Species	*n*	Wet mass (g)	Lean mass (g)	Lean dry mass (g)	Lipid mass (g)	Lipid %	Wing (mm)	Fat score	Water %
Common yellowthroat	30	9.99 ± 1.15	7.05 ± 0.88	2.83 ± 0.23	1.23 ± 0.60	28.64 ± 10.57	53.93 ± 3.42	2.63 ± 1.22	59.6 ± 3.5
Ovenbird	19	19.12 ± 1.52	12.91 ± 1.30	5.10 ± 0.25	2.52 ± 1.14	31.84 ± 9.78	73.95 ± 1.99	2.90 ±1.49	60.2 ± 2.9
Swainson's thrush	22	31.62 ± 2.48	22.00 ± 2.23	8.27 ± 0.47	3.77 ± 1.69	29.88 ± 10.32	96.68 ± 3.29	2.36 ± 1.65	62.1 ± 3.8

Table 2.2. Pearson's correlation coefficients of lipid mass with predictor variables. * = $P \leq 0.001$, ** = $P \leq 0.0001$.

Species	*n*	Body mass	Wing chord	Mass/wing chord	Fat score	Water %
Common yellowthroat	30	0.68**	−0.01	0.73**	0.75**	−0.81**
Ovenbird	19	0.81**	−0.15	0.81**	0.75*	−0.92**
Swainson's thrush	22	0.78**	0.29	0.71*	0.85**	−0.92**

Table 2.3. Partial correlation coefficients of lipid mass with body mass, wing chord, and fat score obtained from multiple regressions. * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$.

Species	Body mass	Wing chord	Fat score
Common yellowthroat	0.54**	−0.39*	0.60***
Ovenbird	0.67**	−0.31	0.59**
Swainson's thrush	0.70***	0.01	0.82***

Table 2.4. Coefficients of determination (r^2, r^{2b}), absolute error (g), and percent error of regression models for predicting lipid mass (LM).

Equation[a]	r^2	r^{2b}	Absolute error[b]	Percent error[b]
Common yellowthroat				
A: LM = 34.090 − 0.665W + 3.397BM + 0.263FS − 170.641MW	0.74	0.59	0.25 ± 0.06	30.1 ± 17.0
B: LM = −1.82 + 0.243FS + 13.027MW	0.69	0.62	0.25 ± 0.08	27.5 ± 10.6
Ovenbird				
A: LM = −177.323 + 2.304W − 8.555BM + 0.326FS + 665.053MW	0.88	0.77	0.33 ± 0.09	15.1 ± 5.0
B: LM = −6.506 + 0.425BM + 0.312FS	0.76	0.63	0.44 ± 0.14	18.7 ± 5.1
Swainson's thrush				
A: LM = 15.297 − 0.235W + 1.067BM + 0.615FS − 73.361MW	0.87	0.82	0.44 ± 0.17	17.3 ± 11.6
B: LM = −7.458 + 0.620FS + 0.309BM	0.87	0.84	0.41 ± 0.15	14.6 ± 7.4

[a] Regression equations include all of the condition indices (A), and indices selected by forward selection (B). BM = body mass, W = wing chord, FS = fat score, MW = mass / wing chord.

[b] Coefficients of determination and lipid mass prediction errors from cross-validation tests. Error values are means ± 95% CI.

CHAPTER III

STOPOVER REFUELING PERFORMANCE OF MIGRATORY LANDBIRDS IN THE NEW YORK METROPOLITAN AREA[2]

INTRODUCTION

The amount of fuel long-distance migrant songbirds can carry during migratory flights is constrained by the need to minimize transport costs as well as the need to maintain the ability to fly (Berthold 2001). Most species cannot complete migration in one flight and instead must repeatedly stop to replenish nutrient stores. The availability of adequate stopover habitat is therefore critical for successful and timely migrations (Moore et al. 1995). As such, widespread human activity and associated habitat loss along migratory flyways has heightened conservation concern for many migratory species (Mehlman et al. 2005, Kirby et al. 2008, Carlisle et al. 2009).

In the New World, the principle migration routes of Nearctic-Neotropical bird species overlap with some of the most densely populated, urbanized regions of North America. City parks and other urban forest fragments often represent the only stopover habitat available to landbird migrants crossing expansive metropolitan areas (Brawn and Stotz 2001, Mehlman et al. 2005, Seewagen 2008). The resulting high concentrations of migrants in these areas during spring and autumn has been well-documented and has made many urban parks popular bird-watching destinations (Fowle and Kerlinger 2001, Milne 2007). Despite recognition of this phenomenon for at least a century (e.g., Chapman 1910), it remains largely unknown whether habitats remaining within cities

[2] A version of this chapter has been submitted to The Condor.

provide migrating birds with the resources they need during stopovers. Urban habitats have the potential to serve as suitable stopover sites that facilitate bird migration but they also have the potential to be energy sinks, luring birds into poor conditions for refueling. The high density at which migrants can occur, and the often degraded habitat conditions in urban parks, may elevate resource competition and constrain the ability of birds to recover energy and nutrient stores. Conversely, urban habitats may confer advantages to migrants. In temperate regions, warmer air temperatures in cities caused by heat-island effects can increase the abundance of terrestrial invertebrates, advance their spring phenology, and prolong their autumn survival (Johnson 2007, Raupp et al. 2010), thereby potentially providing rich food sources to insectivorous birds. Other features of urban habitats may also enhance invertebrate abundance (Kahn and Cornell 1989, Hanks and Denno 1993, McIntyre 2000, Raupp et al. 2010).

Most studies of landbird migrants at urban stopover sites have examined habitat associations and patterns of abundance, richness, and diversity (Brawn and Stotz 2001, Hostettler et al. 2005, Rodewald and Matthews 2005, Pennington et al. 2008). Such measures could provide misleading information about habitat quality (Van Horne 1983, Johnson 2007, Cerasale and Guglielmo 2010), particularly in urban landscapes where migrant stopover site selection is restricted to the little habitat available. High migrant abundance at an urban stopover site cannot be considered indicative of high quality habitat, as it may simply reflect a lack of alternative refugia within the surrounding inhospitable matrix.

A more useful indicator of stopover site quality is the rate at which migrants are able to refuel (Dunn 2000, Guglielmo et al. 2005). I am aware of only two studies that

have taken this approach towards evaluating the quality of urban stopover sites. Seewagen and Slayton (2008) recently provided the first evidence of high-quality habitat in an urban stopover site when several landbird species were shown to gain significant body mass in a New York City park. Similarly, Craves (2009) found *Catharus* thrushes were able to gain significant body mass during stopovers in the city of Dearborn, Michigan. These studies demonstrate that urban habitats have the potential to be suitable landbird stopover sites, but generalization of their findings elsewhere is limited by extreme variation within and among cities in habitat characteristics that likely affect site quality for migrants, such as area, vegetation composition, predators, food availability, and levels of human disturbance. Studies in a diversity of habitats within multiple North American cities will be necessary to better understand the refueling conditions available to Nearctic-Neotropical migrants at urban stopover sites. Here, I expanded previous research in New York City to examine refueling opportunities provided by three urban parks well-known for their use as stopover sites by migratory songbirds.

I employed both a conventional technique based on capture data and a physiological method for measuring the refueling rates of wild birds. The conventional technique examines the relationship between the body mass of single-capture birds and the time of day at which they were captured (e.g., Winker et al. 1992). A significant, positive relationship between these variables indicates that birds captured early in the morning weigh less than those captured later in the day and that diurnal mass gain occurs at the site. The slope of the regression line provides a numerical estimate of the actual mass change rate.

The physiological approach uses blood plasma triglyceride (TRIG) and B-OH-butyrate (BUTY) concentrations to assess the extent to which migrants are replenishing or metabolizing fat stores, respectively (Jenni-Eiermann and Jenni 1994). Circulating TRIG rises in concert with increasing nutrient intake, as newly consumed or synthesized lipids are transported to adipose tissue for storage. Conversely, BUTY concentration decreases in response to feeding and rises during fat oxidation and mass loss. Hence, refueling rate is positively associated with TRIG and negatively associated with BUTY, and both metabolites reflect changes in body mass (Jenni-Eiermann and Jenni 1994, Williams et al. 1999, Cerasale and Guglielmo 2006). Their rapid response to changes in feeding rate allows them to indicate migrant refueling performance at the time and location of sampling (Zajac et al. 2006), thus making metabolite profiling well-suited for field studies of stopover ecology and stopover habitat quality (Schaub and Jenni 2001, Cerasale and Guglielmo 2010, Smith and McWilliams 2010).

An important difference between the body mass-time of day regression technique and plasma metabolite profiling is the former provides a quantitative measure of refueling rate whereas the latter only provides a qualitative, or relative, measure (Guglielmo et al. 2005). Metabolite concentrations of migrants using urban stopover sites are uninformative without reference to birds refueling under different conditions. I therefore examined plasma metabolite levels of migrants in two nearby, but less disturbed, non-urban habitats north of New York City for direct comparison to conspecific migrants stopping over within the city. Similar metabolite profiles between areas would indicate that the urban habitats provide equivalent stopover refueling opportunities as habitats within less modified, suburban areas outside of the city. In

addition to measuring refueling performance, leaf litter arthropod biomass was measured at all sites to assess food abundance for ground-foraging, insectivorous species, such as the ovenbird (*Seiurus aurocapillus*), which I expected to be one of the most common species captured in this study.

METHODS

Study sites

New York City (NYC) is the most populous metropolitan area in the United States (US Census Bureau 2000) and is crossed by four major bird migration routes (Rappole et al. 2000). Large concentrations of migrants regularly occur each spring and autumn in many of the city's parks (Fowle and Kerlinger 2001, Mittelbach and Crewdson 1998). I studied migrants during stopovers in Prospect Park, Inwood Park, and Bronx Park (Fig. 1). These sites were selected with city park officials based on the feasibility of conducting the necessary field research, personal safety, potential for equipment theft and vandalism, potential interference from park visitors and dogs, and habitat similarity (mature, eastern deciduous forest). Each park is an isolated habitat island within heavily urbanized surroundings (Fig. 1).

Prospect Park is a 213 ha public recreational space in the borough of Brooklyn (Kings County) that is visited by more than 6 million people per year (Wells 1998). The park includes mowed lawns and other grassy, open areas, woodland, artificial water bodies, an ice rink, a small zoo on its eastern edge, and a network of asphalt walking paths and official-use roads. Mature deciduous forest represents approximately half of the park's total area (Wells 1998). I captured birds in the area known as "The Ravine"

Figure 3.1. Canopy cover and study site locations in New York City and Westchester County, New York, USA.

(40° 39’ 49” N, -73° 58’ 12” W) within the 100 ha forest in the center of the park (Mittelbach and Crewdson 1998). The Ravine contains an artificial stream, a mature tree community primarily composed of black cherry (*Prunus serotina*), red oak (*Quercus rubra*), tulip poplar (*Liriodendron tulipifera*), and willows (*Salix* spp.), and a woody understory of mostly arrowwood viburnum (*Viburnum dentatum*) and shadbush (*Amelanchier humilis*).

Inwood Park is 80 ha in area and located on the northwestern corner of Manhattan (New York County). The western edge of the park is atop the Hudson River ridge, and then to the east, sharply transitions down into a valley containing mostly tulip poplar (*Liriodendron tulipifera*, Mittelbach and Crewdson 1998, Horenstein 2007). Non-forested recreational facilities are limited to the northeastern corner and encompass approximately ¼ of the park’s total area; the majority of the remaining area is wooded. I captured birds in mature deciduous woods along the ridge, east of Overlook Meadow and west of West Ridge Road (40° 52’ 22” N, -73° 55’ 33” W). Here, the most common trees are black cherry, chestnut oak (*Quercus prinus*), and American ash (*Fraxinus americana*), and the understory is composed mostly of black cherry seedlings and saplings, blackberry (*Rubus* spp.), and arrowwood viburnum (see also Fitzgerald and Loeb 2008).

The grounds of the Bronx Zoo and New York Botanical Garden collectively comprise what is known as Bronx Park, located in Bronx County. Bronx Park is a 229 ha mosaic of natural and partially artificial outdoor animal exhibits, manicured gardens and exotic flora displays, and remaining native forest. The Bronx River bisects the park as it descends south from the Kensico Reservoir in Westchester County towards the East

River. I captured birds in a 4.9 ha section of native forest along the Bronx River on the eastern side of the Bronx Zoo (40° 51’ 6’’ N, -73° 52’ 28’’ W). This area does not contain any animal exhibits or holding facilities, and is not accessible to zoo visitors (see Seewagen and Slayton 2008 for more details).

This site has been examined in earlier studies of migrant stopover ecology (Seewagen 2006, Seewagen and Slayton 2008). Seewagen and Slayton (2008) used the body mass-time of day regression technique to measure refueling rates of migrants captured here 2004 - 2006 and concluded the area represented high-quality stopover habitat. I chose to include this site in the present study, despite this previous finding, because migrant metabolite concentrations and measures of invertebrate biomass from an urban site thought to be high-quality stopover habitat would, in addition to data collected from the non-urban sites, provide useful context in which to view metabolite concentrations and invertebrate biomass at Inwood and Prospect Parks.

Non-urban habitats studied for comparison to the NYC sites were Marshlands Conservancy and Ward Pound Ridge Reservation in Westchester County, New York (hereafter “Westchester”) (Fig 1.). Westchester has a total land area of 1122 km^2, beginning at the northern border of NYC and extending north to Putnam County, east to Connecticut and the Long Island Sound, and west to the Hudson River. Human population density and land cover are strikingly different between Westchester and NYC despite their proximity. Westchester’s population density (850 people/km^2) is only one twelfth of that of NYC (10 464 people/km^2; US Census Bureau 2000), and > 70% of Westchester’s total land area is forest cover, whereas < 20% of NYC’s land area is forest cover (Medley et al. 1995, Cadenasso et al. 2007, Nowak et al. 2007). There is little

difference in forest stand composition, however, between NYC and Westchester (Cadenasso et al. 2007).

The Marshlands Conservancy is a 57 ha wildlife preserve along an inlet of the Long Island Sound 12 km northeast of the NYC border. As a designated sanctuary, recreational activities are limited to trail walking and dogs are not permitted. The sanctuary contains a mix of salt marsh, shrub/scrub, open field, and mature deciduous forest habitats (Wells 1998). I captured birds in the forested area behind the welcome center and east of the large field (40° 57' 14'' N, -73° 42' 8'' W). Mature American beech (*Fagus grandifolia*) and American sweetgum (*Liquidambar styraciflua*) trees create a tall, closed canopy and a shaded, open understory. A stream passes through the area and feeds a nearby pond.

The Ward Pound Ridge Reservation (hereafter "Pound Ridge") is 1746 ha and the county's largest park (Wells 1998). It is 41 km north of the NYC border and spans the towns of Lewisboro and Pound Ridge. Much of the park is former farmland that began to succeed into hardwood forest in the 1920's. Wetlands, marshes, evergreen stands, and meadows and old fields are also represented. The topography is varied and includes hills, ridges, stream valleys, and Cross River Mountain. Recreational facilities are limited to camping shelters, picnic areas, and 50 km of hiking and horseback riding trails (Wells 1998). I captured birds in deciduous woods between Old Schoolhouse and Michigan Roads, and west of the Michigan Road camping shelters (41° 15' 1'' N, -73° 36' 5'' W). The area contains a slow ephemeral stream and moist areas covered in mosses and eastern skunk cabbage (*Symplocarpus foetidus*). Highbush blueberry (*Vaccinium corymbosum*) is prevalent in the understory and red maple (*Acer rubrum*), American

hornbeam (*Carpinus caroliniana*), and black gum (*Nyssa sylvatica*) are the dominant mature tree species.

Study species

Data were collected from several forest-dwelling, nocturnally migrating passerines commonly found in NYC during spring and autumn. Ten species provided large enough sample sizes for plasma metabolite comparisons and/or body mass-time of day regressions: veery (*Catharus fuscescens*), Swainson's thrush (*C. ustulatus*), hermit thrush (*C. guttatus*), wood thrush (*Hylocichla mustelina*), black-throated blue warbler (*Dendroica caerulescens*), yellow-rumped warbler (*D. coronata*), black and white warbler (*Mniotilta varia*), ovenbird, Northern waterthrush (*Seiurus novaborasensis*), common yellowthroat (*Geothlypis trichas*), and white-throated sparrow (*Zonotrichia albicollis*).

I place emphasis on the ovenbird because this species ultimately had sufficient sample sizes across study sites in both seasons and allowed for the most robust analyses. The ovenbird is a long-distance migrant that breeds across much of Canada and the eastern United States, and over-winters throughout Central America and the Caribbean islands (Van Horn and Donovan 1994). Ovenbirds inhabit forests during all periods of their life cycle and are most commonly observed on the ground where they forage for leaf litter arthropods (Stenger 1958, Van Horn and Donovan 1994, Burke and Nol 1998). Ovenbirds do not nest in NYC (DeCandido and Allen 2005, NYSBBA 2007) and only nest in Westchester in relatively low abundance (NYSBBA 2007, Sauer et al. 2008).

Bird capture and blood sampling

Spring and autumn migrants were passively captured at each study site in 6 - 10 mist nets during 1-31 May and 8 September-20 October in 2007 and 2008. Nets were operated from approximately sunrise-11:00 EST for 3-4 days / week in NYC and 5 days / week in Westchester. Each site in Westchester had its own field crew of two individuals, whereas two other field crews of two to three individuals each shared coverage of the three NYC study sites. Capture effort was higher in Westchester because of greater difficulty obtaining adequate migrant sample sizes.

Nets were checked approximately every 8 min so blood could be collected before plasma metabolite concentrations significantly responded to a change in feeding state (Guglielmo et al. 2005, Zajac et al. 2006). Captured birds were assumed to have been in the net the entire time since the net was last checked (i.e., ~8 min), and thus "bleed-time" was conservatively measured as the time elapsed between the previous net check and blood sample collection. Blood was not collected if bleed-time would have exceeded 20 min.

Up to 10 % of calculated total blood volume (Fair et al. 2010) was taken by brachial veinipuncture with a 26-guage needle and collected into one-step, heparinized capillary/centrifuge tubes (Sarstedt microvette CB300). Samples were stored in coolers until nets were closed for the day, and then centrifuged for 5 min. Plasma was transferred to 0.6 mL cryogenic tubes and stored at -80°C for up to 3 months until analysis.

After blood sampling, birds were marked with a USGS aluminum leg band, assigned to age and sex when possible (Pyle 1997), measured (unflattened wing length to

1mm), fat-scored on a 6-point scale (Chapter II), weighed to 0.1g on a digital balance, and released.

Plasma metabolite analyses

Plasma samples were diluted three-fold with 0.9 % NaCl to increase volume. Metabolites were measured on a microplate spectrophotometer (Biotec Powerwave X340) following methods described by Guglielmo et al. (2002, 2005). Briefly, TRIG was determined from the difference of free and triacylglycerol-bound glycerol concentrations during endpoint assay (Sigma, Trinder reagent A and B) and BUTY was directly measured by kinetic endpoint assay (kit E0907979, R-Biopharm). TRIG was analyzed first, followed by BUTY if sufficient sample volume remained. Samples were analyzed in duplicate and values were averaged (all CV < 15 %).

Food abundance

Ovenbirds forage almost exclusively on the forest floor (Holmes and Robinson 1988) and leaf litter arthropod biomass is considered a measure of ovenbird food availability (Burke and Nol 1998, Strong and Sherry 2000). Other migrants I studied, such as the thrush species, also often feed on leaf litter invertebrates (Holmes and Robinson 1988). I collected 0.4 m^2 of leaf litter from the surface to the ground within twelve 1m^2 plots at each site. Plots were spaced every 10 m along two, 60 m transects. Transects were parallel and ~30 m apart. Sampling was conducted between 08:00 and 13:00 EST at the beginning, middle, and end of a field season. Spring arthropods were sampled during 2007 and 2008; autumn arthropods were sampled during 2008 only.

Arthropods were extracted from litter samples in Berlese funnels, identified to order, oven-dried at 60°C for 12 hr, and weighed to 0.0001 g. Individuals that were difficult to see without magnification (< ~1 mm) were considered negligible and not processed. Ovenbirds are unselective foragers and all taxonomic orders of arthropods were assumed to be potential prey (Stenger 1958, Burke and Nol 1998).

Statistical analyses

I used a Chi-square goodness of fit test to compare the number of Nearctic-Neotropical migratory birds captured between each study site, with the null hypothesis being an equal distribution. I first adjusted the number of birds captured at each site for site differences in capture effort (i.e., number of mist nets and hours operated). This was done by averaging the total number of mist net hours (number of mist nets * total number of hours operated) at all five sites and then dividing the actual effort at each individual site by this average to calculate a correction factor. The total number of migrants captured at each site was divided by the correction factor to correct the absolute numbers for equal effort. The Chi-square test was then conducted on the corrected values (Swanson et al. 2003).

Migrant body mass was adjusted to body size (wing length) in each species using a scaled mass model (Peig and Green 2009) unless an initial simple linear regression of body mass and body size was non-significant ($P > 0.05$). I used simple linear regression to examine the relationship between body mass or size-adjusted body mass and capture time (expressed as hours since sunrise) (Winker et al. 1992, Carlisle et al. 2005, Seewagen and Slayton 2008). Hourly mass change rate was obtained from the beta

coefficient. Studies often apply this technique only to species with samples sizes of more than 50 (Jones et al. 2002) or 100 (Dunn 2002, Bonter et al. 2007) birds, but few species in this study had such large sample sizes and I chose a lower criterion of $n \geq 30$ to allow more species to be included in the analyses.

I used general linear models (GLM) with a backwards selection ($\alpha = 0.1$) procedure to identify variables that contributed to site differences in plasma TRIG and BUTY concentrations. Variables examined were capture time, body mass or size-adjusted body mass, Julian date, year, and bleed time. Metabolite concentrations were compared among sites with analysis of covariance (ANCOVA), with variables retained by the GLM entered as covariates (Guglielmo et al. 2005). All covariates met assumptions of equal variance and homogenous slopes. Site differences in metabolites were tested with analysis of variance (ANOVA) when no covariates were identified. Combining TRIG and BUTY into a refueling index with principal components analysis (e.g., Schaub and Jenni 2001, Guglielmo et al. 2005) did not qualitatively change site comparison results and I therefore only report the results of the aforementioned analyses of TRIG and BUTY individually. Age and sex could not be considered because sample sizes at some sites were small, most of the species examined cannot be reliably sexed in the field, and the ageing and sexing skills of field crew were inconsistent among study sites.

I tested for differences in invertebrate biomass among sites with repeated measures ANOVA to account for multiple sampling sessions throughout a season, with site, time period (early, middle, late), and their interaction entered as fixed factors. Site differences in biomass during each spring time period were compared individually with

ANOVA because of a significant interaction between site and time period in the repeated measures analysis.

Statistical analyses were performed with R version 2.1.0 (R Development Core, Vienna, Austria) and SPSS version 17.0 (SPSS Inc., Chicago, IL). Results were interpreted as significant when $P \leq 0.05$, with the exception of backwards selection procedures where variables were retained at $P < 0.1$. Tukey HSD tests were used for all post-hoc, pairwise comparisons. Non-normal data were $\log_{10}+1$ transformed to meet parametric assumptions. Values are reported as means ± SE.

RESULTS

Relative migrant abundance

Total captures of Nearctic-Neotropical migrants differed significantly among sites during spring and autumn after correcting for equal effort (Table 3.1); more migrants were captured in Prospect Park than at any other site. On average, spring and autumn migrants were captured in NYC at more than triple the rate they were captured in Westchester (Fig. 2).

Hourly mass change

Eight Nearctic-Neotropical migrant species had a sufficient sample size ($n \geq 30$) from at least one study site during spring or autumn to investigate the relationship between body mass and capture time. Sample sizes and regression statistics are presented in Table 3.2.

Spring.— In Prospect Park, ovenbirds and black-throated blue warblers gained 0.33 and 0.18 g hr^{-1}, respectively, whereas common yellowthroat, Northern waterthrush,

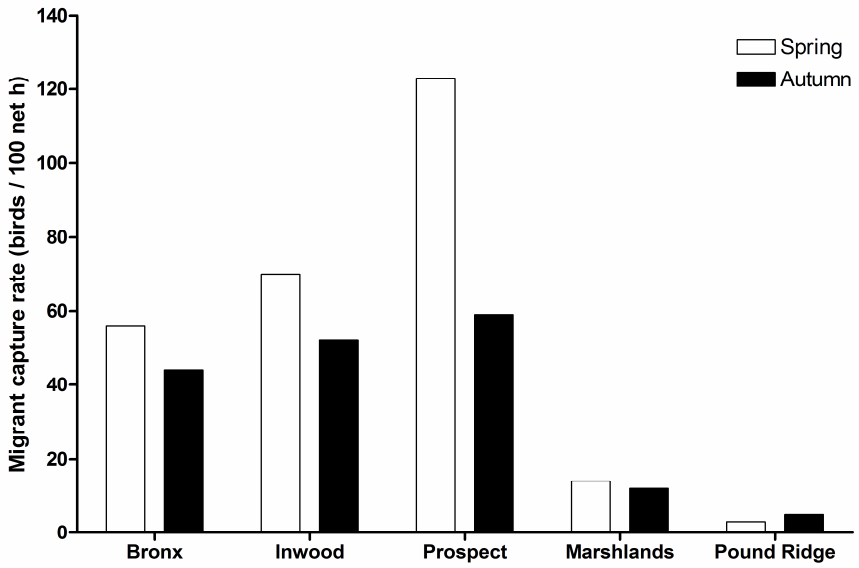

Figure 3.2. Capture rates of Nearctic-Neotropical migratory landbirds at stopover sites in New York City (Bronx, Inwood, Prospect) and Westchester County (Marshlands, Pound Ridge), New York, 2007-2008. Capture rate expressed as number of migratory birds captured per 100 net hours and calculated as (total migrants captured / total net hours) x 100. One net hour is equivalent to one mist net operated for one hour.

and black and white warbler body mass did not significantly change over time. Ovenbird, yellow-rumped warbler, and common yellowthroat body mass did not change over time in Inwood Park (all $P > 0.24$). Ovenbird and common yellowthroat gained mass in Bronx Park (0.45 and 0.24 g hr^{-1}, respectively); Northern waterthrush did not (Table 3.2).

Autumn.— In Prospect Park, the relationship between body mass and capture time was non-significant in the veery, Swainson's thrush, or common yellowthroat, and approached significance ($P = 0.06$) in the white-throated sparrow (Table 3.2). White-throated sparrow body mass was unrelated to capture time in Inwood and Bronx Parks. Black-throated blue warbler did not show changes in body mass in Inwood Park, and Northern waterthrush and common yellowthroat did not show changes in body mass in Bronx Park (Table 3.2). Mass gain in the yellow-rumped warbler was not significant at Inwood Park and approached significance ($P = 0.07$) at Marshlands Conservancy. Common yellowthroat did not gain significant mass at Marshlands Conservancy (Table 3.2). No other species had adequate sample sizes from Westchester to examine mass changes.

Plasma metabolites

A sufficient number of blood samples for site comparisons was obtained from six species: Swainson's thrush, hermit thrush, wood thrush, yellow-rumped warbler, ovenbird, and common yellowthroat. Mean metabolite values and sample sizes for all species sampled are shown in Table 3.3. Variables identified as significant covariates and controlled for in site comparisons differed among species (Table 3.4). TRIG was

positively associated, and BUTY was negatively associated, with time of capture in most species, reflecting the transition from overnight fasting or flight to morning feeding.

Ovenbird TRIG and BUTY concentrations did not differ among sites during spring (TRIG: $F_{4,128} = 0.5$, $P = 0.73$; BUTY: $F_{4,113} = 1.2$, $P = 0.32$; Fig. 3.3). No other spring migrants provided a sufficient sample size ($n \geq 5$) from at least one non-urban site to allow meaningful statistical comparisons to the urban sites. Ovenbird TRIG concentrations were also not different among sites during autumn ($F_{3,68} = 0.5$, $P = 0.68$). Ovenbird BUTY during autumn differed overall among sites ($F_{3,67} = 3.0$, $P = 0.04$), with birds at Marshlands Conservancy having generally lower levels than birds in NYC, but no pairwise comparisons were significant (all $P > 0.07$; Fig. 3.4). There were significant site differences in Swainson's thrush TRIG concentrations during autumn ($F_{4,64} = 2.7$, $P = 0.04$); in post-hoc tests, TRIG concentrations of birds in the NYC sites and the Marshlands Conservancy were higher than those of birds at Pound Ridge (all $P < 0.04$) but were not different from each other (all $P > 0.08$; Fig. 3.4). Autumn BUTY levels of Swainson's thrush were not different among sites ($F_{4,63} = 0.7$, $P = 0.60$; Fig. 3.4). TRIG concentrations of yellow-rumped warbler differed among sites during autumn ($F_{3,84} = 4.2$, $P = 0.01$), with concentrations at Inwood Park and the two Westchester sites higher than at Bronx Park (all $P < 0.05$) but not different from each other (all $P > 0.1$; Fig. 3.4). Yellow-rumped warbler BUTY also differed among sites ($F_{3,80} = 11.7$, $P < 0.001$), with highest levels at Inwood Park and lowest levels at Pound Ridge (Fig. 3.4). Common yellowthroat TRIG was not different among sites during autumn ($F_{3,96} = 0.3$, $P = 0.84$), whereas BUTY was different ($F_{3,92} = 3.0$, $P = 0.04$) and generally lower in NYC than in Westchester (Fig. 3.4). Autumn TRIG and BUTY concentrations did not differ among

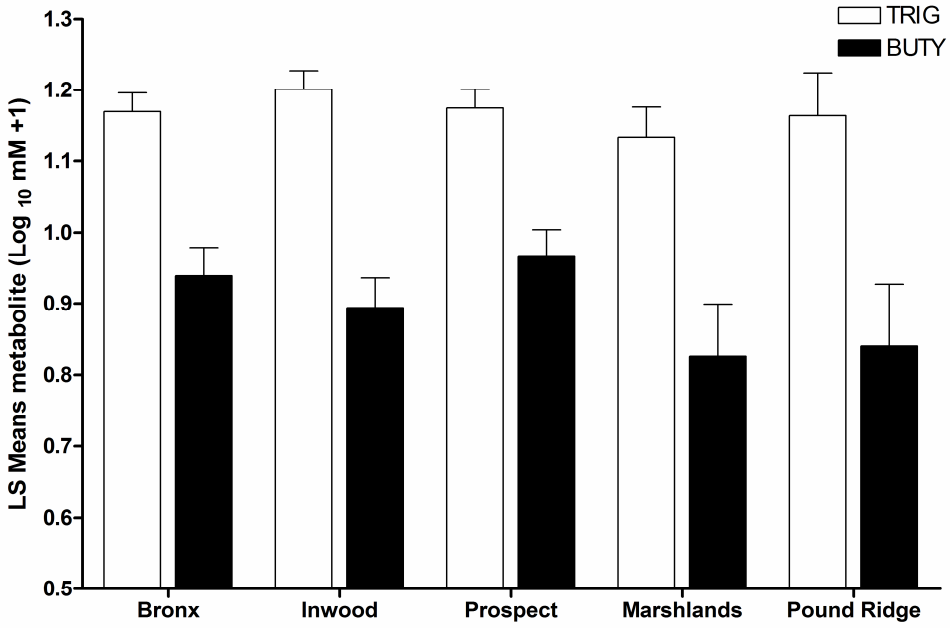

Figure 3.3. Plasma triglyceride (TRIG) and B-OH-butyrate (BUTY) concentrations of ovenbirds at stopover sites in New York City (Bronx, Inwood, Prospect) and Westchester County (Marshlands, Pound Ridge), New York, during spring 2007-2008. Metabolite values expressed as least squares means + SE controlling for covariates (Table 4). Sample sizes reported in Table 3.2.

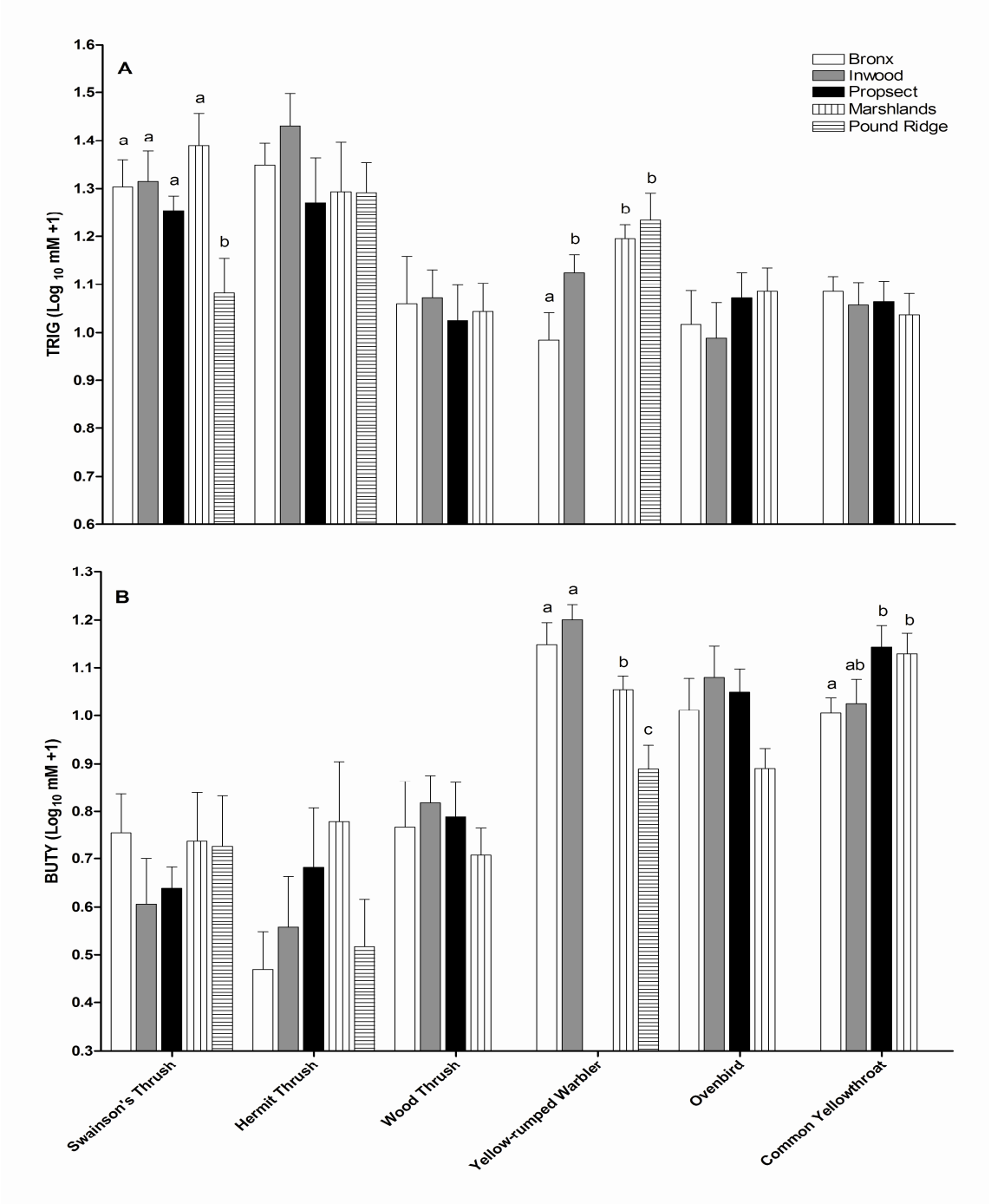

Figure 3.4. Plasma triglyceride (TRIG [A]) and B-OH-butyrate (BUTY [B]) concentrations of landbird migrants at stopover sites in New York City (Bronx, Inwood, Prospect) and Westchester County (Marshlands, Pound Ridge), New York, during autumn 2007-2008. Metabolite values are least squares means + SE when covariates were controlled for and means + SE when no covariates were identified (Table 3.4). Letters indicate significant site differences within a species. Sample sizes reported in Table 3.2.

sites in hermit thrush (TRIG: $F_{4,39} = 1.0$, $P = 0.45$; BUTY: $F_{4,37} = 1.4$, $P = 0.26$) or wood thrush (TRIG: $F_{3,41} = 0.1$, $P = 0.97$; BUTY: $F_{3,41} = 0.7$, $P = 0.59$; Fig. 3.4).

Food abundance

Total arthropod biomass was primarily represented by 11 orders during spring: Diplopoda (26%), Isopoda (14%), Coleoptera (13%), Lepidoptera (11%), Chilopoda (10%), Hymenoptera Formcidae (5%), other Hymenoptera (4%), Hemiptera (4%), Araneae (3%), Lepidoptera larva (3%), and Diptera (2%). During autumn, total arthropod biomass was primarily represented by 10 orders: Diplopoda (19%), Isopoda (17%), Coleoptera (16%), Hemiptera (12%), Lepidoptera (9%), Orthoptera (8%), Araneae (7%), Collembola (5%), Diptera (2%), and Opiliones (2%). The proportion of most orders was similar among sites (Table 3.5).

Trends in arthropod biomass throughout the spring were highly inconsistent among sites (site*time period interaction: $F_{8, 345} = 2.8$, $P = 0.005$); at some sites biomass increased, whereas at others it decreased or remained similar (Fig. 3.5). There were significant site differences in arthropod biomass early ($F_{4,115} = 2.6$, $P = 0.04$) and late ($F_{4,115} = 3.4$, $P = 0.01$) in the spring, but not during the middle of the season ($F_{4,115} = 0.8$, $P = 0.56$). During early spring, biomass in Bronx Park was marginally higher than in Inwood Park ($P = 0.06$), but no pairwise comparisons were significant. Biomass was significantly greater in Inwood Park than in Bronx ($P = 0.03$) and Prospect Parks ($P = 0.05$) late in the spring.

During autumn, the effects of the site*time period interaction and time period were not significant (interaction: $F_{8,165} = 1.6$, $P = 0.12$; time period: $F_{2,173} = 0.8$, $P =$

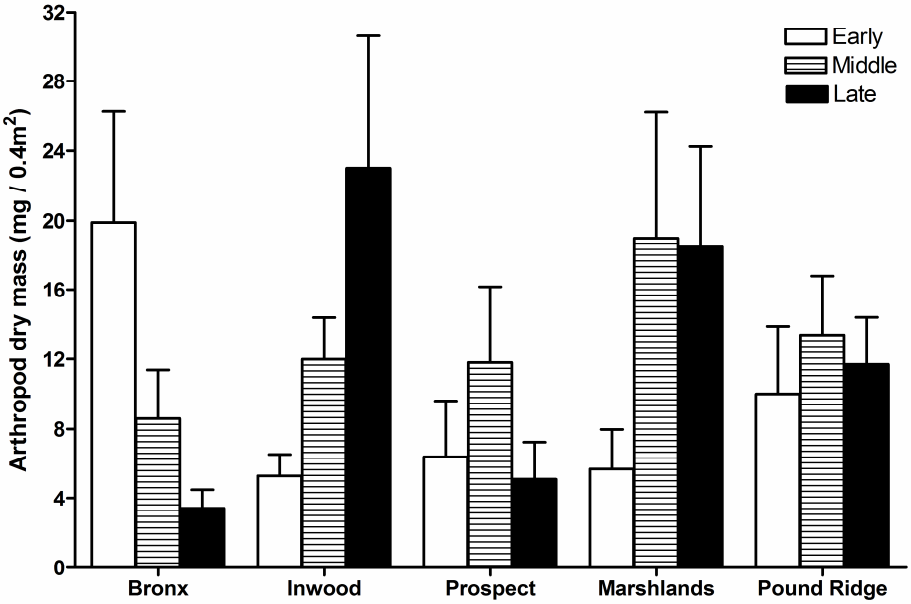

Figure 3.5. Mean + SE arthropod dry mass in 0.4m^2 leaf litter samples collected from migratory bird stopover sites in New York City (Bronx, Inwood, Prospect) and Westchester County (Marshlands, Pound Ridge), New York, over three time periods during spring 2007-2008. Arthropod dry mass was significantly greater at Inwood Park than at Bronx and Prospect Parks late in the spring; no other pairwise comparisons of sites within a time period were significant.

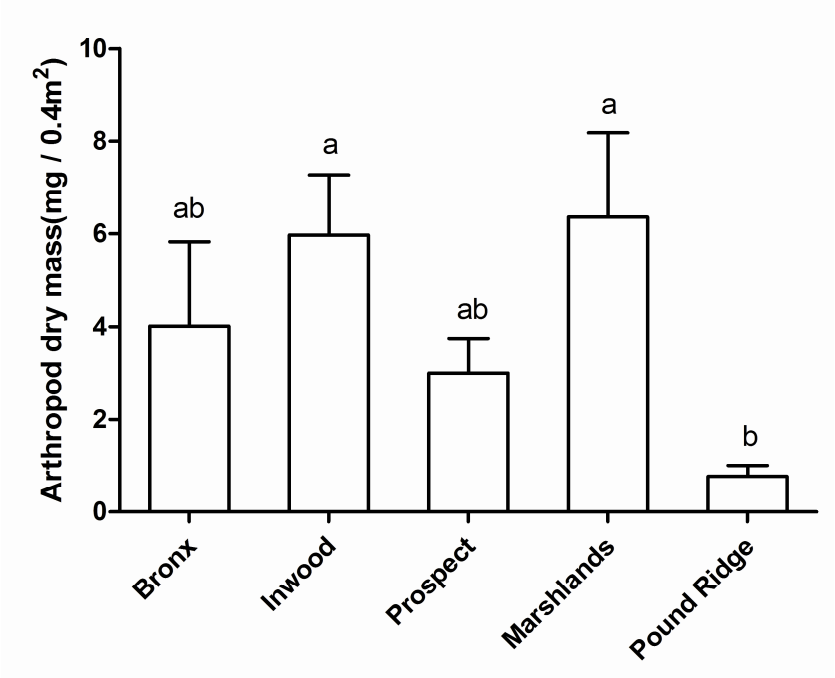

Figure 3.6. Mean + SE arthropod dry mass in 0.4m^2 leaf litter samples collected from migratory bird stopover sites in New York City (Bronx, Inwood, Prospect) and Westchester County (Marshlands, Pound Ridge), New York, during autumn 2008. In contrast to spring (Fig. 3.5), data from three sampling periods were pooled because of a non-significant site*time period interaction. Letters indicate significant site differences.

0.47) and sequentially dropped from the model. Average arthropod biomass across all time periods was significantly different among sites ($F_{4,175} = 2.9$, $P = 0.02$), with biomass being significantly lower at Pound Ridge than Marshlands Conservancy ($P = 0.03$) and Inwood Park ($P = 0.05$; Fig. 3.6).

DISCUSSION

This is to my knowledge the first application of plasma metabolite profiling and measures of food abundance to assess the relative quality of stopover sites for passerines in an urbanized landscape. Many city parks are famous for receiving exceptional concentrations of migrants (Fowle and Kerlinger 2001, Mehlman et al. 2005, Milne 2007); yet the resources provided by such habitats, and hence their true value as stopover sites, has been questioned.

Urban ecosystems often support greater terrestrial invertebrate biomass than non-urban habitats because of warmer microclimates and various other habitat characteristics (Raupp et al. 2010 and references within), which in turn could benefit insectivorous migratory birds refueling at urban stopover sites. In this study, site differences during spring were dependent on the time of season, but at no point was there a consistent trend for higher leaf litter arthropod biomass in the urban habitats than in the non-urban habitats. There was also no indication that biomass was greater in the urban sites during autumn, although the site farthest outside NYC, Pound Ridge, had the lowest biomass. Food abundance for ovenbirds and similar ground-foraging, insectivorous migrants does not appear to differ overall between habitats in NYC and Westchester.

Bird capture rates indicated a dramatic difference in the density of landbird migrants in NYC and Westchester during both spring and autumn. High migrant density in urban habitats is a common phenomenon in cities along major migration routes and likely results from the limited habitat availability in urban landscapes. Indeed, the percentage of forest cover in NYC is less than one third that of Westchester and migrants become concentrated in its small forest patches. In addition, earlier spring greening and delayed autumn dormancy of vegetation by as much as two weeks in urban forests due to heat-island effects (Roetzer et al. 2000, White et al. 2002, Zhang et al. 2004a, b) and differing phenology of exotic plants that are common to disturbed habitats (Shustack et al. 2009) may actually attract migrants to urban stopover sites. Vegetation phenology appears to be an important cue used during stopover site selection by in-flight migrants, as it can provide information about food availability (McGrath et al. 2009, Strode 2009). Spring greening was noticeably later, and autumn leaf fall was noticeably earlier in Westchester than in NYC during the study period (pers. obs.) and possibly contributed to the disparity in migrant densities.

Resource competition and territory defense have been observed in passerine migrants during stopover (Rappole and Warner 1976, Bibby and Green 1980, Dierschke et al. 2005, Buler 2006; but see Fasola and Fraticelli 1990) and mass gain can be density-dependent (Moore and Yong 1991, Kelly et al. 2002, Cerasale and Guglielmo 2010). For example, Cerasale and Guglielmo (2010) found that food abundance was comparable between stopover sites with native vegetation and those dominated by exotic salt cedar (*Tamarix* spp.) in the western U.S., but Wilson's warblers (*Wilsonia pusilla*) were in fact able to refuel at higher rates in the salt cedar habitats possibly because of lower

competitor density. In my study, ovenbird TRIG concentrations were not different between NYC and Westchester during spring or autumn, suggesting equal refueling rates despite the extreme difference in migrant density and similar food abundance across sites. Other species also indicated comparable refueling rates in NYC and Westchester even though competition was likely greater in the urban sites. It is unknown, however, how food abundance compared among sites for some of these species that have varying diets and forage at other strata besides the forest floor (e.g., yellow-rumped warbler).

Plasma metabolites of migrants in NYC can be further interpreted through comparisons to other studies in non-urban areas. Ovenbird TRIG levels in NYC during spring and autumn were higher than the average TRIG concentrations of ovenbirds over-wintering in Jamaica (Brown 2006); presumably, nutrient intake of ovenbirds on wintering grounds is only what is needed to maintain energy balance, and the higher TRIG levels of ovenbirds during migratory stopover in NYC indicate energy accumulation above minimum metabolic requirement. I am unaware of any reports of TRIG concentrations in migrating ovenbirds. Average TRIG levels of spring migrant Swainson's thrushes were higher at Inwood and Prospect Parks than at a stopover site considered to be of high-quality in Ontario, Canada (Guglielmo et al. 2005). Average TRIG levels of spring migrant yellow-rumped warblers were two to three-fold higher in NYC than at a national wildlife refuge in northwestern Ohio (MacDade 2009). During autumn, yellow-rumped warblers at Bronx and Inwood Parks had comparable average TRIG levels to conspecifics during stopovers in Rhode Island, and hermit thrushes had higher average TRIG levels in NYC than in Rhode Island (Smith and McWilliams 2010). The average TRIG concentration of autumn Swainson's thrushes at each NYC site was

higher than or similar to the TRIG concentrations of migrating Swainson's thrushes in northern California (Leist 2007). Similar TRIG levels between NYC and these studies in non-urban areas further indicate the NYC sites offer adequate, and possibly high quality, refueling conditions for landbird migrants.

In several cases there was no relationship between migrant body mass and time of day, which may have resulted from inadequate sample sizes. The body mass-time of day regression technique requires large sample sizes to detect mass change trends because of the great variation in body mass among individuals at a given time of day (Winker et al. 1992, Dunn 2000), and some studies have therefore chosen to only investigate species with sample sizes of more than 100 birds (Dunn 2002, Bonter et al. 2007). In this study, most sample sizes were less than 50 birds. Capturing birds during only the morning hours may also explain why changes in body mass over time were not always detected. The regression technique is more often applied to banding data collected over longer daytime periods (e.g., Dunn 2001, Jones et al. 2002, Morris et al. 2003, Bonter et al. 2007). Mass gain during the short sampling period in this study may have been too subtle to result in significant relationships between body mass and time of capture. This is particularly so during autumn when the sampling period was shorter than spring because of later sunrise times. Species that did in fact have significant relationships between body mass and time of day in the NYC sites gained mass at comparable, and in most cases higher, rates as conspecifics in non-urban areas (Winker et al. 1992, Dunn 2001, Bonter et al. 2007). These mass gain rates were also similar to those measured in Bronx Park in an earlier study (Seewagen and Slayton 2008).

The need to recover expended energy stores is perhaps the greatest constraint faced by *en route* migrants, and the rate at which migrants are able to refuel is a common indicator of stopover habitat quality (Dunn 2000, Guglielmo et al. 2005, Seewagen and Slayton 2008, Cerasale and Guglielmo 2010). In this study, the refueling opportunities for migrants in the urban sites did not appear to be any poorer than those in the less disturbed, suburban habitats. Plasma metabolite values indicated comparable refueling performance of migrants in NYC and Westchester, and measures of arthropod biomass suggested similar food abundance for ground-foraging insectivores in the two areas during both seasons. Further, plasma metabolite levels and arthropod biomass in Prospect and Inwood Parks were similar to Bronx Park, where previous research suggested high quality stopover habitat is available (Seewagen and Slayton 2008). TRIG levels in NYC were similar to, or higher than, those reported in the literature for migrants in various non-urban areas. Regressions also indicated mass gain occurred at rates comparable to or higher than non-urban habitats elsewhere. Taken together, my results suggest sufficient refueling opportunities are available in NYC and add to a growing body of evidence that urban habitats can represent suitable stopover sites for migratory landbirds (Seewagen and Slayton 2008, Craves 2009, Matthews and Rodewald 2010, Chapter VI).

LITERATURE CITED

Berthold P (2001) Bird migration: a general survey. Oxford University Press, New York.

Bibby CJ, Green RE (1980) Foraging behaviour of migrant pied flycatchers, *Ficedula hypoleuca*, on temporary territories. Journal of Animal Ecology 49:507-521.

Bonter DN, Donovan TM, Brooks EW (2007) Daily mass changes in landbirds during migration stopover on the south shore of Lake Ontario. Auk 124:122-133.

Brawn JD, Stotz DF (2001) The importance of the Chicago region and the "Chicago Wilderness" initiative for avian conservation. Pp. 509-522 in: Avian ecology and conservation in an urbanizing world (Marzluff JM, Bowman R, Donnelly R, eds). Kluwer Press, Boston.

Brown DR (2006) Food supply and the dry-season ecology of a tropical resident bird community and an over-wintering migrant bird species. Dissertation. Tulane University, New Orleans, LA.

Buler JJ (2006) Understanding habitat use by landbirds during migration along the Mississippi Gulf Coast using a scale-dependent approach. Dissertation. University of Southern Mississippi, Hattiesburg, MS.

Burke DM, Nol E (1998) Influence of food abundance, nest-site habitat, and forest fragmentation on breeding ovenbirds. Auk 115:96-104.

Cadenasso ML, Pickett STA, McDonnell MJ, Pouyat RV (2007) Forest vegetation along an urban-rural gradient in the New York City metropolitan area: patterns and relationships to ecosystem processes. Transactions of the Linnaean Society of New York 10:79-99.

Carlisle JD, Kaltenecker GS, Swanson DL (2005) Stopover ecology of autumn landbird migrants in the Boise foothills of southwestern Idaho. Condor 107:244-258.

Carlisle JD, Skaken SK, Kus BE, van Riper III C, Paxton KL, Kelly JF (2009) Landbird migration in the American West: recent progress and future research directions. Condor 111:211-225.

Cerasale DJ, Guglielmo CG (2006) Dietary effects on prediction of body mass changes in birds by plasma metabolites. Auk 123:836-846.

Cerasale DJ, Guglielmo CG (2010) An integrative assessment of the effects of tamarisk on stopover ecology of a long-distance migrant along the San Pedro River, Arizona. Auk 127:636-646.

Chapman F (1910) Birds of the vicinity of New York City. American Museum Journal 6:81-102.

Craves JA (2009) A fifteen year study of fall stopover patterns of *Catharus* thrushes at an inland, urban site. Wilson Journal of Ornithology 121:112-118.

DeCandido R, Allen D (2005) First confirmed nesting of the Pine Warbler (*Dendroica pinus*) in New York City. Kingbird 55:328-334.

Dierschke V, Mendel B, Schmaljohann H (2005) Differential timing of spring migration in northern wheatears *Oenanthe oenanthe*: hurried males or weak females? Behavioral Ecology and Sociobiology 57:470-480.

Dunn EH (2000) Temporal and spatial patterns in daily mass gain of Magnolia Warblers during migratory stopover. Auk 117:12-21.

Dunn EH (2001) Mass change during migration stopover: a comparison of species groups and sites. Journal of Field Ornithology 72:419-432.

Dunn EH (2002) A cross-Canada comparison of mass change in birds during migration

stopover. Wilson Bulletin 114:368-379.

Fair J, Paul E, Jones J (2010) Guidelines to the use of wild birds in research. Ornithological Council, Washington D.C.

Fasola M, Fraticelli F (1990) Non-competitive habitat use by foraging passerine birds during spring migrations. Ethology, Ecology and Evolution 2:363-371.

Fitzgerald JM, Loeb RE (2008) Historical ecology of Inwood Hill Park, Manhattan, New York. Journal of the Torrey Botanical Society 135:281-293.

Fowle M, Kerlinger P (2001) The New York City Audubon Society guide to finding birds in the metropolitan area. Cornell University Press, New York.

Guglielmo CG, O'Hara PD, Williams TD (2002) Extrinsic and intrinsic sources of variation in plasma lipid metabolites of free living western sandpipers. Auk 119:437-445.

Guglielmo CG, Cerasale DJ, Eldermire C (2005) A field validation of plasma metabolite profiling to assess refueling performance of migratory birds. Physiological and Biochemical Zoology 78:116-125.

Hanks LM, Denno RF (1993) Natural enemies and plant water relations influence the distribution of an armored scale insect. Ecology 74:1081-1091.

Holmes RT, Robinson SK (1998) Spatial patterns, foraging tactics, and diets of ground foraging birds in a northern hardwood forest. Wilson Bulletin 100:377-394.

Horenstein S (2007) Inwood Hill and Isham Parks: geology, geography, and history. Transactions of the Linnaean Society of New York 10:1-54.

Hostetler M, Duncan S, Paul J (2005) Post-construction effects of an urban development on migrating, resident, and wintering birds. Southeastern Naturalist 4:421-434.

Jenni-Eiermann S, Jenni L (1994) Plasma metabolite levels predict individual body mass changes in a small long-distance migrant, the garden warbler. Auk 111:888-899.

Johnson EA (2007) A seasonal guide to New York City's invertebrates. American Museum of Natural History, New York.

Johnson MD (2007) Measuring habitat quality: a review. Condor 109:489-504.

Jones JC, Francis M, Drew M, Fuller S, Ng MWS (2002) Age-related differences in body mass and rates of mass gain of passerines during autumn migratory stopover. Condor 104:49-58.

Kahn D, Cornell HV (1989) Leafminers, early leaf abscission, and parasitoids: a tritrophic interaction. Ecology 70:1219-1226.

Kelly JF, DeLay LS, Finch DM (2002) Density-dependent mass gain by Wilson's warblers during stopover. Auk 119:210-213.

Kirby JS, Stattersfield AJ, Butchart SHM, Evans MI, Grimmett RFA, Jones VR, O'Sullivan J, Tucker GM, Newton I (2008) Key conservation issues for migratory land- and waterbird species on the world's major flyways. Bird Conservation International 18:49-73.

Leist AJ (2007) The importance of fruit to Swainson's thrushes, *Catharus ustulatus*, during fall migration: a field test of plasma metabolite analysis. Thesis. Humboldt State University, Arcata, CA.

MacDade LS (2009) Dietary contribution of emergent aquatic insects and consequences for refueling in spring migrant songbirds. Thesis. Ohio State University, Columbus, OH.

Matthews S, Rodewald P (2010) Movement behaviour of a forest songbird in an

urbanized landscape: the relative importance of patch-level effects and body condition during migratory stopover. Landscape Ecology 25:955-965.

McGrath LJ, van Riper III C, Fontaine JJ (2009) Flower power: tree flowering phenology as a settlement cue for migrating birds. Journal of Animal Ecology 78:22-30.

McIntyre NE (2000) Ecology of urban arthropods: a review and a call to action. Annals of the Entomological Society of America 93:825-835.

Medley KE, McDonnell MJ, Pickett STA (1995) Forest-landscape structure along and urban to rural gradient. Professional Geographer 47:159-168.

Mehlman DW, Mabey SE, Ewert DN, Duncan C, Abel B, Cimprich D, Sutter RD, Woodrey MS (2005) Conserving stopover sites for forest-dwelling migratory landbirds. Auk 122:1281-1290.

Milne P (2007) Where to watch birds in world cities. Yale University Press, New Haven, CT.

Mittelbach M, Crewdson M (1998) Wild New York: A guide to the wildlife, wild places, and natural phenomena of New York City. Random House, New York.

Moore FR, Gauthreaux SA, Kerlinger P, Simons TR (1995) Habitat requirements during migration: important link in conservation. Pp. 121-144 in: Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues (Martin TE, Finch DM, eds). Oxford University Press, New York.

Moore FR, Yong W (1991) Evidence of food-based competition among passerine migrants during stopover. Behavioral Ecology and Sociobiology 28:85-90.

Morris SR, Pusateri CR, Battaglia KA (2003) Spring migration and stopover ecology of common yellowthroats on Appledore Island, Maine. Wilson Bulletin 115:64-72.

Nowak DJ, Hoehn RE, Crane DE, Stevens JC, Walton JT (2007) Assessing urban forest effects and values: New York City's urban forest. Resource Bulletin NRS-9. U.S. Department of Agriculture, Forest Service, Northern Research Station, Syracuse, NY.

New York State Breeding Bird Atlas (NYSBBA) 2000-2005 (2007) Breeding bird atlas data and maps. http://www.dec.ny.gov/animals/51030.html. Accessed April 2010.

Peig J, Green AJ (2009) New perspectives for estimating body condition from mass/length data: the scaled index as an alternative method. Oikos 118:1883-1891.

Pennington DN, Hansel J, Blair RB (2008) The conservation value of urban riparian areas for landbirds during spring migration: land cover, scale, and vegetation effects. Biological Conservation 141:1235-1248.

Pyle P (1997) Identification guide to North American birds, part 1. Slate Creek Press, Bolinas, CA.

Rappole JH, Warner DW (1976) Relationships between behavior, physiology and weather in avian transients at a migration stopover site. Oecologia 26:193-212.

Rappole JH, Derrickson SR, Hubàlek Z (2000) Migratory birds and spread of West Nile Virus in the western hemisphere. Emerging Infectious Diseases 6:319-328.

Raupp MJ, Shrewsbury PM, Herms DA (2010) Ecology of herbivorous arthropods in urban landscapes. Annual Review of Entomology 55:19-38.

Rodewald PG, SN Matthews (2005) Landbird use of riparian and upland forest stopover habitats in an urban landscape. Condor 107:259-268.

Roetzer T, Wittenzeller M, Haeckel H, Nekovar J (2000) Phenology in central Europe-

differences and trends of spring phenophases in urban and rural areas. International Journal of Biometeorology 44:60-66.

Sauer JR, Hines JE, Fallon J (2008) The North American Breeding Bird Survey, results and analysis 1966-2007. http://www.mbr- pwrc.usgs.gov/bbs/bbs.html. Accessed March 2010.

Schaub M, Jenni L (2001) Variation of fueling rates among sites, days and individuals in migrating passerine birds. Functional Ecology 15:584-594.

Seewagen CL (2006) The energetics and stopover ecology of Neotropical migrant passerines in an urban park. Thesis. Columbia University, New York, NY.

Seewagen CL (2008) Lipid content of Nearctic-Neotropical migratory passerines killed during stopovers in a New York City park. Northeastern Naturalist 15:87-96

Seewagen CL, Slayton EJ (2008) Mass changes of migratory landbirds during stopovers in a New York City park. Wilson Journal of Ornithology 120:296-303.

Shustack DP, Rodewald AD, Waite TA (2009) Springtime in the city: exotic shrubs promote earlier greenup in urban forests. Biological Invasions 11:1357-1371.

Smith SB, McWilliams SR (2010) Patterns of fuel use and storage in migrating passerines in relation to fruit resources at autumn stopover sites. Auk 127:108-118.

Stenger J (1958) Food habits and available food of ovenbirds in relation to territory size. Auk 75:335-346.

Strode PK (2009) Spring tree species use by migrating yellow-rumped warblers in relation to phenology and food availability. Wilson Journal of Ornithology 121:457-468.

Strong AM, TW Sherry (2000) Habitat-specific effects of food abundance on the condition of ovenbirds wintering in Jamaica. Journal of Animal Ecology 69:883-895.

Swanson DL, Carlisle HA, Liknes ET (2003) Abundance and richness of Neotropical migrants during stopover at farmstead woodlots and associated habitats in southeastern South Dakota. American Midland Naturalist 149:176-191.

US Census Bureau (2000) State and county quick facts. http://quickfacts.census.gov/qfd/ Accessed April 2010.

Van Horne B (1983) Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.

Van Horn MA, Donovan TM (1994) Ovenbird (*Seiurus aurocapillus*). No. 182 in: The Birds of North America (Poole A, Gill F, eds). Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C.

Wells JV (1998) Important Bird Areas of New York State. National Audubon Society, New York.

White MA, Nemani RR, Thornton PE, Running SW (2002) Satellite evidence of phenological differences between urbanized and rural areas of the eastern United States deciduous broadleaf forest. Ecosystems 5:260-277.

Williams TD, Guglielmo CG, Egeler O, Martyniuk CJ (1999) Plasma lipid metabolites provide information on mass change over several days in captive Western sandpipers. Auk 116:994-1000.

Winker K, Warner DW, Weisbrod AR (1992) Daily mass gains among woodland migrants at an inland stopover site. Auk 109:853-862.

Zajac RM, Cerasale DJ, Guglielmo CG (2006) The rapid response of plasma metabolites to changes in feeding rate in a small passerine Wilson's warbler *Wilsonia pusilla*. Journal of Avian Biology 37:405-408.

Zhang X, Friedl MA, Schaaf CB, Strahler AH, Schneider A (2004a) The footprint of urban climates on vegetation phenology. Geophysical Research Letters 31:L12209. doi:10.1029/2004GL020137.

Zhang X, Friedl MA, Schaaf CB, Strahler AH (2004b) Climate controls on vegetation phonological patterns in northern mid- and high latitudes inferred from MODIS data. Global Change Biology 10:1133-1145.

Table 3.1. Total captures of Nearctic-Neotropical migratory landbirds during spring and autumn 2007-2008 in New York City (Bronx, Inwood, Prospect) and Westchester County (Marshlands, Pound Ridge), New York. Capture totals were significantly different between sites after correcting for equal effort (see Methods).

Study site	Season	Net hr	Absolute captures	Corrected captures	χ^2_4	*P*
	Spring					
Bronx		739	413	521		
Inwood		798	557	650		
Prospect		531	654	1148	1604	< 0.001
Marshlands		1428	206	135		
Pound Ridge		1165	37	30		
	Autumn					
Bronx		1204	534	723		
Inwood		1235	640	845		
Prospect		738	437	966	1131	< 0.001
Marshlands		2219	267	196		
Pound Ridge		2759	135	80		

Table 3.2. Mean ± SE body mass and diurnal mass changes of migratory landbirds during stopovers in New York City (Bronx, Inwood, Prospect) and Westchester County (Marshlands), New York, 2007-2008. Hourly mass change rates determined from beta coefficients of linear regressions of body mass and capture time when $P \leq 0.1$. Mass change only examined when $n \geq 30$.

Species	Site	Season	*n*	Body mass (g)	r^2	*P*	g hr^{-1}	% mean mass hr^{-1}
Veery	Prospect	Autumn	46	33.6 ± 0.5	0.05	0.15		
Swainson's thrush	Prospect	Autumn	37	31.8 ± 0.5	0.00	0.97		
Black-throated blue warbler	Inwood	Autumn	40	9.4 ± 0.1	0.05	0.16		
	Prospect	Spring	39	10.2 ± 0.1	0.13	0.03	0.18 ± 0.08	1.8
Yellow-rumped warbler	Inwood	Spring	32	13.5 ± 0.2	0.00	0.91		
		Autumn	58	11.9 ± 0.1	0.01	0.61		
	Marshlands	Autumn	48	11.8 ± 0.1	0.08	0.07	0.30 ± 0.16	2.5
Black and white warbler	Prospect	Spring	44	11.0 ± 0.1	0.05	0.14		
Ovenbird	Bronx	Spring	44	21.0 ± 0.2	0.20	0.003	0.45 ± 0.14	1.0
	Inwood	Spring	41	20.0 ± 0.2	0.02	0.29		
	Prospect	Spring	102	20.6 ± 0.2	0.05	0.03	0.33 ± 0.15	1.6
Northern waterthrush	Bronx	Spring	33	18.1 ± 0.3	0.04	0.29		
		Autumn	35	18.6 ± 0.4	0.00	0.80		
	Prospect	Spring	98	18.1 ± 0.2	0.00	0.79		
Common yellowthroat	Bronx	Spring	41	11.0 ± 0.1	0.14	0.02	0.24 ± 0.10	2.2
		Autumn	57	10.2 ± 0.1	0.00	0.83		
	Inwood	Spring	38	11.1 ± 0.1	0.02	0.48		
	Prospect	Spring	80	10.6 ± 0.1	0.01	0.47		
		Autumn	32	10.2 ± 0.2	0.02	0.43		
	Marshlands	Autumn	37	10.0 ± 0.1	0.01	0.60		
White-throated sparrow	Bronx	Autumn	106	26.1 ± 0.2	0.01	0.43		
	Inwood	Autumn	41	26.0 ± 0.8	0.01	0.65		
	Prospect	Autumn	43	24.9 ± 0.3	0.08	0.06	0.41 ± 0.21	1.6

Table 3.3. Mean ± SE plasma triglyceride (TRIG) and B-OH-butyrate (BUTY) concentrations (mmol L^{-1}) of migratory landbirds during stopovers in New York City and Westchester County, New York, 2007-2008. Sample sizes shown in parentheses.

		New York City						Westchester County			
		Bronx Park		Inwood Park		Prospect Park		Marshlands Conservancy		Ward Pound Ridge Reservation	
Species	Season	TRIG	BUTY	TRIG	BUTY	TRIG	BUTY	TRIG	BUTY	TRIG	BUTY
Veery	Spring	-	-	-	-	-	-	-	-	-	-
	Autumn	2.41 (1)	0.21 (1)	-	-	1.83 ± 0.39 (9)	0.85 ± 0.15 (9)	2.16 (1)	0.66 (1)	1.41 ± 0.22 (4)	0.92 ± 0.16 (4)
Swainson's thrush	Spring	2.07 ± 0.14 (27)	0.69 ± 0.06 (25)	3.01 ± 0.52 (18)	0.74 ± 0.06 (18)	2.21 ± 0.32 (16)	0.66 ± 0.07 (16)	2.32 ± 0.30 (3)	0.86, 0.93 (2)	2.05, 3.00 (2)	0.92, 0.33 (2)
	Autumn	2.52 ± 0.62 (10)	0.66 ± 0.11 (10)	2.03 ± 0.24 (8)	0.63 ± 0.14 (8)	2.01 ± 0.13 (35)	0.52 ± 0.06 (35)	2.61 ± 0.65 (7)	0.54 ± 0.06 (7)	1.24 ± 0.18 (6)	0.69 ± 0.22 (6)
Hermit thrush	Spring	-	-	-	-	-	-	-	-	-	-
	Autumn	2.53 ± 0.29 (16)	0.37 ± 0.07 (13)	3.16 ± 0.53 (8)	0.45 ± 0.12 (7)	2.12 ± 0.48 (5)	0.50 ± 0.07 (5)	1.64 ± 0.17 (5)	0.71 ± 0.20 (5)	2.17 ± 0.34 (8)	0.37 ± 0.07 (8)
Wood thrush	Spring	2.43 ± 0.38 (7)	0.53 ± 0.07 (7)	1.69 ± 0.15 (13)	0.70 ± 0.10 (11)	1.65 ± 0.26 (4)	0.71 ± 0.15 (4)	1.68 ± 0.43 (4)	0.68 ± 0.10 (4)	3.42 ± 1.73 (3)	0.92, 0.64 (2)
	Autumn	1.30 ± 0.33 (5)	0.88 ± 0.34 (5)	1.28 ± 0.14 (14)	0.68 ± 0.06 (14)	1.12 ± 0.14 (9)	0.67 ± 0.10 (9)	1.35 ± 0.28 (14)	0.55 ± 0.06 (14)	1.06 ± 0.24 (3)	0.77 ± 0.16 (3)
Yellow-rumped warbler	Spring	1.86 ± 0.23 (11)	1.07 ± 0.22 (8)	3.04 ± 0.25 (27)	1.01 ± 0.12 (20)	2.05 ± 0.29 (9)	1.07 ± 0.18 (6)	2.16 ± 0.39 (4)	0.81 (1)	-	-
	Autumn	0.85 ± 0.13 (12)	1.54 ± 0.20 (12)	1.53 ± 0.11 (31)	1.79 ± 0.17 (31)	0.42 (1)	1.59 (1)	1.75 ± 0.12 (36)	1.20 ± 0.07 (33)	1.75 ± 0.17 (12)	0.81 ± 0.06 (11)
Ovenbird	Spring	1.65 ± 0.11 (35)	1.03 ± 0.11 (33)	1.52 ± 0.09 (34)	0.96 ± 0.09 (29)	1.67 ± 0.11 (40)	1.02 ± 0.11 (37)	1.48 ± 0.22 (15)	0.85 ± 0.16 (10)	2.05 ± 0.78 (7)	0.60 ± 0.23 (7)

	Autumn	1.14 ± 0.10 (14)	1.07 ± 0.19 (12)	1.33 ± 0.54 (11)	1.40 ± 0.29 (11)	1.50 ± 0.37 (21)	1.28 ± 0.17 (21)	1.46 ± 0.17 (28)	0.94 ± 0.09 (28)	0.75 ± 0.04 (4)	1.46 ± 0.29 (4)
Northern water-thrush	Spring	1.95 ± 0.18 (33)	1.03 ± 0.11 (29)	3.76 ± 2.34 (7)	1.01 ± 0.27 (6)	1.63 ± 0.09 (57)	1.16 ± 0.09 (52)	1.83 ± 0.43 (4)	1.12 ± 0.21 (4)	-	-
	Autumn	1.47 ± 0.14 (31)	1.08 ± 0.12 (31)	1.28 ± 0.22 (3)	1.05 ± 0.17 (3)	1.42 ± 0.18 (20)	1.21 ± 0.13 (20)	1.65 ± 0.49 (4)	1.19 ± 0.31 (4)	-	-
Common yellow-throat	Spring	2.39 ± 0.59 (26)	0.98 ± 0.13 (21)	2.56 ± 0.40 (25)	1.03 ± 0.15 (17)	1.66 ± 0.14 (28)	1.46 ± 0.21 (20)	1.42 ± 0.26 (4)	1.12 ± 0.16 (3)	-	-
	Autumn	1.43 ± 0.12 (38)	1.08 ± 0.08 (38)	1.48 ± 0.40 (18)	1.18 ± 0.14 (16)	1.26 ± 0.12 (21)	1.47 ± 0.12 (19)	1.10 ± 0.08 (22)	1.63 ± 0.20 (21)	0.55 (1)	0.97 (1)
White-throated sparrow	Spring	2.30 ± 0.43 (13)	0.97 ± 0.11 (13)	1.94 (1)	2.17 (1)	1.48 ± 0.23 (4)	2.35 ± 0.65 (3)	1.62 (1)	1.08 (1)	-	-
	Autumn	1.44 ± 0.10 (69)	1.24 ± 0.09 (67)	1.75 ± 0.21 (39)	1.66 ± 0.24 (38)	1.70 ± 0.14 (36)	1.50 ± 0.16 (33)	1.76 ± 0.21 (4)	1.39 ± 0.20 (4)	1.31 ± 0.32 (4)	1.90 ± 0.37 (4)

Table 3.4. Variables retained by general linear models with backwards selection and included as covariates in study site comparisons of metabolites. TRIG = triglyceride, BUTY = B-OH-butyrate, B = bleed time, D = Julian date, M = body mass, T = time since sunrise, Y = year. Positive or negative symbols indicate direction of effect. Ovenbird was the only species with a sufficient sample size to examine during spring. All species listed were examined during autumn; dashes indicate that no variables explained significant variation in plasma metabolite concentration.

	Spring		Autumn	
Species	TRIG	BUTY	TRIG	BUTY
Swainson's thrush			+T	-T, +Y
Hermit thrush			+T, -B	-
Wood thrush			-	-
Yellow-rumped warbler			+T, +D	+M
Ovenbird	+T, -Y, +D, -B	-T, +B	+T, +Y, +M	-T, +D
Common yellowthroat			+T, -Y	-T

Table 3.5. Percentage of total leaf litter arthropod dry mass represented by each taxonomic order at migratory landbird stopover sites in New York City (Bronx, Inwood, Prospect) and Westchester County (Marshlands, Pound Ridge), New York, spring (S) and autumn (A) 2007-2008.

	Bronx		Inwood		Prospect		Marshlands		Pound Ridge	
Order	S	A	S	A	S	A	S	A	S	A
Acari			< 1		< 1		< 1		< 1	
Araneae	< 1	4	5	13	5	3	< 1	2	6	37
Blattodea	< 1	< 1		5						
Chilopoda	15	< 1	15	1	6		8		5	
Coleoptera	5	6	10	7	14	14	16	30	17	21
Coleoptera larvae	< 1		1				1		< 1	
Collembola	< 1	2	< 1	11	< 1	1	< 1	4	2	5
Dermaptera	< 1		< 1		< 1		< 1		5	
Diplopoda	34	2	24	18	3	28	32	28	27	7
Diplura						< 1				
Diptera	< 1	7	< 1	1	1		2		5	1
Diptera larvae	< 1		< 1		< 1				< 1	
Hemiptera	< 1	32	< 1	10	1	4	5	3	12	25
Homoptera		< 1								3
Hymenoptera	13		4	1	3		< 1	2	1	
Hymenoptera formcidae	16		2	< 1	4	< 1	3	1	4	
Isopoda	5	14	24	22	42	22	6	14	7	
Isoptera			1				2			< 1
Lepidoptera	9	14	9	< 1	16	3	18	15	3	< 1
Lepidoptera larvae	< 1		1		4		5		2	
Opiliones	< 1			8						
Orthoptera		17	2		< 1	25	< 1		< 1	
Pseudo-scorpionies			< 1	< 1				< 1	< 1	
Thysanoptera			< 1				< 1		1	
Thysanura	< 1									
Unknown			< 1						< 1	

CHAPTER IV

USE OF QUANTITATIVE MAGNETIC RESONANCE ANALYSIS AND A MORPHOMETRIC PREDICTIVE MODEL TO INVESTIGATE LEAN BODY MASS CHANGES IN NEARCTIC-NEOTROPICAL PASSERINES AT AN URBAN STOPOVER SITE[1]

INTRODUCTION

Most bird species undergo considerable fluctuations in body mass during migration, as mass is repeatedly lost during energetically-demanding flights and replenished during stopover refueling. The energy density of fat is several-fold higher than that of protein and carbohydrates, and birds are unique among vertebrates in their ability to sustain high-intensity aerobic exercise primarily with fatty acid oxidation (McWilliams et al. 2004). It was at one time believed that changes in body mass of migrant birds were due to changes in fat mass alone (Odum et al. 1964), but more recently it has become clear that lean tissues can also significantly contribute to total body mass dynamics (Piersma 1990, Lindström and Piersma 1993, Karasov and Pinshow 1998).

Much of the evidence for lean mass changes during migration comes from shorebirds that have been shown to lose substantial organ and muscle mass during flight, which is later restored on stopover (e.g., Piersma et al. 1999). Atrophy of organs that are not needed during flight, such as digestive tract components, may be an adaptation to lower power requirements and basal metabolic rate, and in turn, increase energy efficiency (Jenni and Jenni-Eiermann 1998, Piersma and Gill 1998, Biebach and

[1] A version of this chapter has been accepted for publication by the Journal of Comparative Physiology B (Seewagen and Guglielmo 2010).

Bauchinger 2003, Landys-Ciannelli et al. 2003), or may simply be a beneficial consequence of the relatively high turnover rates of these organs (Bauchinger and McWilliams 2009). Losses in flight muscle mass that accompany decreasing power requirements throughout a flight as birds become lighter may act to further economize energy expenditure (Pennycuick 1998, Lindström et al. 2000, Biebach and Bauchinger 2003). The steady supply of citric acid cycle intermediates needed for fat oxidation also necessitates the catabolism of some protein during flight (Jenni and Jenni-Eiermann 1998). Another potential benefit of protein breakdown is an increased liberation of water under dehydrating flying conditions (Jenni and Jenni-Eiermann 1998).

A bird's rate of protein loss during flight is a function of the size of its remaining fat stores. The rate is greatest when fat stores drop below 5-10% of total body mass (Jenni et al. 2000, Schwilch et al. 2002). In absolute terms, the amount of protein catabolized is parallel to the amount of fat catabolized (Bauchinger and Biebach 1998). Perhaps for these reasons extreme fluctuations in lean body mass are best known in shorebirds which make exceptionally long non-stop flights and come close to exhausting fat stores relative to other groups of migratory birds. Passerines, in contrast, migrate in shorter bouts and likely reach critically low fat stores only when crossing large expanses of inhospitable habitat such as oceans and deserts. It is these geographical barriers that push passerine migrants towards maximum capacity on endogenous energy sources, and therefore, it is at these crossings we would expect to observe the most substantial changes in passerine lean mass. Indeed, most of the literature on lean mass dynamics in free-living passerines concerns Palearctic migrants before or after crossing the Sahara Desert (e.g., Karasov and Pinshow 1998, Deerenberg et al. 2002, Schwilch et al. 2002, Biebach and

Bauchinger 2003, Bauchinger et al. 2005). For example, Karasov and Pinshow (1998) estimated that lean mass accounted for as much as 37% of total body mass gains in blackcaps (*Sylvia atricapilla*) refueling after crossing the Sahara. Schwilch et al. (2002) showed that total lean body mass and individual organ and muscle masses were significantly reduced in birds that had just crossed the Sahara Desert and Mediterranean Sea compared to conspecifics migrating through continental Europe. Bauchinger et al. (2005) similarly found garden warblers (*Sylvia borin*) that had just crossed the Sahara had lower organ and muscle masses than garden warblers preparing to cross. Such studies provide strong evidence that passerine migrants incur significant protein loss during passage over large geographical barriers, and subsequent stopover refueling includes the deposition of both fat and lean mass.

Under less demanding situations when stopover habitat is more contiguous, however, it less certain how much lean tissue passerines catabolize in flight and rebuild during stopovers (Åkesson et al. 1992, Bauchinger and Biebach 2005). Between the Great Lakes and Gulf of Mexico, for example, there are no significant barriers impeding forest-dwelling, Nearctic-Neotropical migratory passerines in eastern North America (Tankersley and Orvis 2003). Metropolitan and agricultural areas may be thought of as anthropogenic barriers (Moore et al. 1995, Mehlman et al. 2005), but even the largest urban and agricultural landscapes are incomparable in size to natural barriers like the Sahara Desert and the Gulf of Mexico, and usually have several habitat fragments within that can be used as stopover sites when needed (Swanson et al. 2003, Mehlman et al. 2005, Seewagen and Slayton 2008).

In this study, I examined lean mass variation in migratory passerines during stopovers in New York City (NYC), USA, where no major barriers exist immediately to the north or south, and most migrants arrive with ample fat stores remaining (Seewagen 2008, Seewagen and Slayton 2008). Lean mass dynamics have seldom been studied in New World passerine species or in passerines at a stopover site that is not in close proximity to a large geographical barrier. As it has only recently been demonstrated that migrants can successfully refuel during stopovers in heavily developed, urbanized landscapes (Seewagen and Slayton 2008, Craves 2009, Chapter III), an additional goal of this study was to learn whether lean mass contributed to total body mass changes previously observed in birds at my urban study sites. Determining the extent to which lean tissues are involved in stopover refueling is important for understanding the most important nutrient sources that stopover habitats must provide (Karasov and Pinshow 1998).

I used two sources of body composition data to explore lean mass variation in Nearctic-Neotropical migrants. The first was obtained by quantitative magnetic resonance (QMR) analysis of birds captured during autumn 2008 in Bronx Park, NYC. QMR analysis is a fast, accurate, non-invasive technique for directly measuring the fat and wet lean body mass of small vertebrates (Taicher et al. 2003, Jones et al. 2009, McGuire and Guglielmo in press), including passerine birds (Guglielmo, Gerson, McGuire, and Seewagen, unpublished data). The second data set was obtained by using an existing predictive model (Chapter II) to estimate, based on total body mass and visible subcutaneous fat score, the fat mass of birds captured during spring 2007-2008 in Bronx Park and Prospect Park, NYC when the QMR unit was unavailable. With these datasets I

examined (1) the proportion of variance in total body mass explained by lean body mass, after controlling for body size, (2) hourly rates of fat and lean body mass change during stopover refueling, and (3) fat and lean mass changes in recaptured birds.

METHODS

Study sites

NYC is crossed by the Atlantic migration routes of many Nearctic-Neotropical passerine species and its parks are well-known for receiving large concentrations of passage migrants (Mittlebach and Crewdson 1998, Fowle and Kerlinger 2001). Bronx and Prospect Parks are primarily composed of mature, eastern deciduous forest and provide suitable stopover habitat for migrating passerines (Seewagen and Slayton 2008, Chapter III, VI). Stopovers at these sites often span multiple days (Chapter V, VI).

Data collection

Data were collected from spring and autumn migrants mist-netted from sunrise until approximately 11:00 EST, 1-31 May and 8 September-20 October, 2007-2008. All birds were weighed to the nearest 0.1g and fat-scored on a 6-point scale (Chapter II). Unflattened wing length was measured to 1 mm and birds were banded with aluminum USGS leg bands.

The body composition of birds captured in Bronx Park during autumn 2008 was determined by QMR analysis as follows. Conscious birds were scanned within 45 min of capture and banding in a QMR unit (Echo-MRI, Echo Medical Systems, Houston, TX) housed in a customized mobile laboratory (Glendale Recreational Vehicles, Strathroy,

ON) at the study site. Birds were scanned in duplicate on the 'small bird' and 'two-accumulation' settings of the Echo-MRI software, yielding measures of fat mass and wet lean body mass to 0.001 g. Total scanning time was ~4 min per individual. Raw QMR fat mass data were transformed using calibration equations for small birds developed with house sparrows (*Passer domesticus*) and zebra finches (*Taeniopygia guttata*) in a laboratory validation study (Guglielmo, Gerson, McGuire, and Seewagen, unpublished data). Validation indicated the relative error for predictions of fat and wet lean mass were ± 11% and ± 1.5%, respectively. It should be noted that in QMR analysis, wet lean body mass does not include non-fat components such as skeleton or feathers and in this way differs from fat-free body mass provided by traditional chemical extraction. However, the two are highly correlated.

Study species

I analyzed QMR data from the gray catbird (*Dumetella carolinensis*), hermit thrush (*Catharus guttatus*), and white-throated sparrow (*Zonotrichia albicollis*) because these were the migratory passerines that provided the largest sample sizes (n >20). Sample sizes of all other species were < 10 birds which I considered inadequate for statistical analyses.

Gray catbird is a widespread migrant that breeds across most of the U.S. and winters from the coastal mid-Atlantic U.S. to the Neotropics (Cimprich and Moore 1995). The white-throated sparrow's breeding range spans the U.S.-Canada border east of the Rocky Mountains and its wintering range extends from New England to Florida and Texas (Falls and Kopachena 2010). Eastern populations of the hermit thrush breed

throughout the northeastern U.S. and the majority of Canada south of the tree-line, and primarily over-winter from New Jersey and the mid-Atlantic states to southern Florida (Jones and Donovan 1996). Although gray catbirds nest and white-throated sparrows over-winter in NYC (pers. obs.), I assumed all of the individuals in our samples were on migration. There were no between-season or between-year recaptures of the gray catbirds or white-throated sparrows used in this study, nor were any individuals recaptured within the autumn 2008 season which increased my confidence they did not remain in the study site to nest or over-winter.

I used the predictive model to study body composition changes in ovenbirds (*Seiurus aurocapillus*). The ovenbird is a long-distance Neotropical migrant that breeds across much of Canada and the eastern U.S., and over-winters throughout Central America and the Caribbean islands. Ovenbirds do not nest or over-winter in NYC (Van Horn and Donovan 1994, DeCandido and Allen 2005). I used this species because it had the largest sample sizes of the species with an available model for estimating the fat mass of living birds and it gained total body mass during stopovers in Bronx and Prospect Parks.

Data analyses

I used SPSS 17.0 (SPSS Inc., Chicago, IL) for all analyses and accepted significance at $P \leq 0.05$. All data met normality assumptions.

Fat, lean, and total body mass data that were significantly correlated with wing length were size-adjusted using a scaled mass index (Peig and Green 2009). The scaled mass index, unlike multiple regression with a size measurement included as an additional

independent variable, allowed me to control for the effects of body size on both the independent and dependent variables. Another attractive characteristic of the scaled mass index is that, unlike mass-length residuals (Green 2001), it retains original units of measurement.

QMR measurements.— After controlling for structural size, I regressed fat and lean body mass against total body mass to determine the proportion of the variation in total body mass explained by these two components (Piersma and Jukema 1990, Piersma and Van Brederode 1990, Wirestam et al. 2008). I used major axis (MA) type II regression to find the line of best fit through the data because the independent variable likely contained error, variables were measured in the same units, and the slope of the line was of foremost interest (Sokal and Rohlf 1981, Warton et al. 2006). This and similar regression approaches to body composition data have received criticism for overestimating the influence of lean mass on total body mass variation (Lindström and Piersma 1993, van der Meer and Piersma 1994) and are also unable to determine whether lean body mass differences among birds at a stopover site are due to preexisting differences upon arrival, or increases in lean mass during the stopover period. I therefore conducted the following additional analyses to determine whether migrants gained lean mass during stopover refueling at my study sites.

First, I used linear regression to relate fat and lean body mass to time of capture (expressed as hours since sunrise). A significant, positive relationship between lean body mass and capture time would indicate that birds captured early in the morning have lower lean body mass than those captured later in the day, and diurnal lean mass gain occurs at the site. This is analogous to the widely used technique of measuring total body mass

changes in passerines during stopover, whereby a regression of total body mass and time of capture is used to estimate an hourly mass gain rate (e.g., Dunn 2000, 2001; Carlisle et al. 2005; Bonter et al. 2007, Seewagen and Slayton 2008).

Second, I calculated net changes in the fat and lean body mass of birds that were recaptured one day or more after their initial capture and that had gained at least 1 g of total body mass between captures.

Predictive model.— I used a predictive model (Chapter II) to estimate, based on total body mass and visible subcutaneous fat score, the fat mass of ovenbirds captured during spring research seasons at Bronx and Prospect Parks when the QMR unit was unavailable. Simple linear regressions of estimated fat mass and total body mass against time of capture were then used to quantify hourly rates of fat and total body mass gain; the difference between the slopes was taken to represent the contribution of lean mass to gains in total body mass.

RESULTS

I captured and analyzed with QMR 31 gray catbirds, 21 hermit thrushes, and 40 white-throated sparrows (total body mass of one sparrow was not recorded due to scribe error) during autumn in Bronx Park. With the predictive model I estimated the fat mass of 43 and 102 ovenbirds captured during spring in Bronx and Prospect Parks, respectively. Fat mass as a percentage of total body mass upon capture was on average 13% in gray catbirds, 9% in hermit thrushes, and 11% in white-throated sparrows during autumn in Bronx Park, and 15% in ovenbirds in both Bronx and Prospect Parks during spring (Table 4.1).

Fat and lean contributions to total mass variation

Fat and lean body mass were significantly related to total body mass in the gray catbird (Table 4.2). Regression coefficients were weak, however, leading to poor slope estimates for fat and lean that illogically sum to far greater than 1. Stronger relationships of fat and lean body mass with total body mass were found in the hermit thrush and white-throated sparrow (Table 4.2). Fat and lean body mass respectively increased 0.50 and 0.53 g per 1 g of total body mass in the hermit thrush. Regression slopes indicated that white-throated sparrows increased 0.42 g in fat mass and 0.48 g in lean body mass per 1 g increase in total body mass (Table 4.2). Fat and lean slopes in these species also do not sum to exactly 1 which I assume is due to error surrounding QMR measurements and/or size-adjustment procedures.

Hourly mass changes

The relationship between lean body mass and capture time was significant in the gray catbird ($r^2 = 0.21$, df = 1, 29, $P = 0.010$) and marginally significant in the white-throated sparrow ($r^2 = 0.09$, df = 1, 38, $P = 0.058$), and indicated rates of lean body mass gain of 1.123 g h^{-1} and 0.320 g h^{-1}, respectively. Lean body mass was unrelated to capture time in the hermit thrush ($r^2 = 0.02$, df = 1, 19, $P = 0.49$). Fat mass was not related to capture time in any species (gray catbird: $r^2 = 0.08$, df = 1, 29, $P = 0.13$; white-throated sparrow: $r^2 = 0.01$, df = 1, 38, $P = 0.59$; hermit thrush: $r^2 = 0.08$, df = 1, 19, $P = 0.22$).

Ovenbird total body mass was significantly related to time of capture at Bronx Park ($r^2 = 0.20$, df = 1, 41, $P = 0.003$) and increased 0.45 g h^{-1}. Fat mass was also

significantly related to capture time (r^2 = 0.17, df = 1, 41, P = 0.006), increasing 0.29 g h^{-1} and accounting for 64% of the increase in total body mass. At Prospect Park, ovenbird total body mass and fat mass were significantly, yet weakly, related to time of capture (total body mass: r^2 = 0.05, df = 1, 100, P = 0.029; fat: r^2 = 0.06, df = 1, 100, P = 0.018). Total body mass increased 0.33 g h^{-1}, of which an estimated 0.17 g h^{-1} (52%) was fat.

Recaptured birds

Eight migrants were recaptured and reanalyzed with QMR. Four of these birds (3 hermit thrushes and 1 ovenbird) refueled and gained at least 1 g of total body mass between captures. One hermit thrush gained mostly fat, whereas the other two had increases in lean mass that accounted for 28% and 65% of their total body mass increase (Table 4.3). The ovenbird gained 1.831 g of lean body mass between captures which represented 44% of its total body mass increase.

DISCUSSION

A wealth of evidence indicates that lean tissues are dynamic during bird migration. However, studies of lean mass changes in free-living migrants have been primarily limited to long-distance migrant shorebirds and Palearctic passerines at the Sahara Desert where they are challenged to make the longest non-stop flight of their migration. Much less is known about lean tissue changes in Nearctic-Neotropical passerine species, or in passerines when stopover habitat is more continuously available and shorter flights are possible (Åkesson et al. 1992, Bauchinger and Biebach 2005). In this study, I observed lean mass changes in Nearctic-Neotropical migratory passerines that had likely flown

only a few hours prior to arrival. Each of the four approaches suggested lean mass was considerably variable and migrants were building lean tissue during stopovers.

The relationships of fat and lean body mass with total body mass were weak in the gray catbird and did not yield informative estimates of the contributions of each tissue to variation in total body mass. However, regression analyses indicated that in hermit thrushes and white-throated sparrows, lean mass accounted for 48-53% of the differences among individuals in total body mass once body size was controlled for. Lean body mass was related to time of day in the gray catbird and white-throated sparrow, indicating accumulation of lean mass during stopover refueling at Bronx Park. Marsh (1983) similarly noted that gray catbird lean mass was greater in the evening than in the morning at a stopover site. Total body mass of ovenbirds in Bronx and Prospect Parks increased at a greater rate than fat mass, suggesting that lean mass accounted for 36-48% of the added total body mass. Despite a small sample size, the recaptured birds perhaps most clearly and conclusively illustrate the extent to which migrants deposited lean mass during stopovers, with lean mass accounting for 28-65% of the total body mass gained in three of the four individuals. The hermit thrush that gained mostly fat was the thrush with the highest lean body mass at first capture, suggesting that lean mass upon arrival may be a primary determinant of how much lean versus fat mass a bird gains during stopover.

The contributions of lean tissue to total body mass variation that I found are comparable to similar field studies of both passerines and shorebirds. For instance, lean tissue accounted for 37% of changes in total body mass in blackcaps refueling after crossing the Sahara Desert (Karasov and Pinshow 1998). Garden warblers lost (and presumably later recovered) up to 50% of their organ and muscle mass during flights

across the Sahara (Bauchinger et al. 2005). Piersma and Van Brederode (1990) estimated that shorebird species preparing to depart African wintering grounds gained 25-45% of their total body mass in the form of lean mass. Lean mass accounted for half of the total body mass increases of bar-tailed godwits (*Limosa lapponica*) staging in the Wadden Sea (Piersma and Jukema 1990). Red knots (*Calidris canutus islandica*) gained 22% of their total body mass as lean mass during stopovers in Iceland (Piersma et al. 1999).

Laboratory studies of exercised or fasted at-rest birds have found that lean mass accounts for similar proportions of total body mass changes as those observed in wild birds. For example, captive garden warblers lost and regained 27% of their body mass as lean mass during fasting and a subsequent recovery period (Klaassen and Biebach 1994). Klaassen et al. (2000) showed that an average of 17% of the mass recovered by a thrush nightingale (*Luscinia luscinia*) following flights in a wind tunnel consisted of protein. Wirestam et al. (2008) found that increases in total body mass exceeded increases in fat mass in a laboratory study of four Palearctic passerine species, and attributed the remaining 36-67% of total body mass accumulation to lean tissues.

Interestingly, the lean body mass of gray catbirds and white-throated sparrows in my study was related to time of day, but fat mass was not. This may reflect a necessary recovery of digestive tract mass lost *en route* to the stopover site before efficient nutrient assimilation and fat deposition could occur (Klaassen and Biebach 1994, Hume and Biebach 1996, Lindström et al. 1999, Piersma et al. 1999). Among the recaptured hermit thrushes, the bird recaptured after only 3 days had a higher relative contribution of lean mass to total mass gain than the birds recaptured after 4-5 days, which also suggests some degree of biphasic mass gain (*sensu* Carpenter et al. 1993). Digestive organs often

undergo the most substantial fluctuations in mass throughout migration (Piersma and Gill 1998, Biebach and Bauchinger 2003), as they are of little functional value during in-flight fasting, but are of utmost importance during stopover refueling. Digestive organs are also likely to decrease in mass early into a flight and ahead of other lean tissues because of their relatively short carbon retention times and high turnover rates (Bauchinger and McWilliams 2009). Hence, digestive organs may represent the most variable lean tissues in short-distance passerine migrants such as hermit thrushes and white-throated sparrows.

CONCLUSION

Although my study sites are not near a geographical barrier, most migrants arrive in NYC with fat stores remaining, and I examined mostly temperate, short-distance migrant species, each of the approaches suggested lean mass changed considerably *en route* to or at my study sites. It is unlikely that large changes in lean mass of passerines are limited to times when birds are forced to make relatively long non-stop flights, when fat stores near depletion, or when energy contributions from other sources are necessary. The use of amino acids for Krebs cycle intermediates and gluconeogensis causes some protein breakdown regardless of flight duration or size of the fat stores (Jenni and Jenni-Eiermann 1998), and may account for the lean mass variation I observed. Further, protein catabolism may actually occur at greater rates during short-distance than long-distance flights (Jenni-Eiermann and Jenni 1991, Jenni and Jenni-Eiermann 1992) because costs of upregulating the mechanisms needed to fuel high intensity aerobic exercise with fat may not be economical for only short time periods (Jenni and Jenni-Eiermann 1998) and there is less urgency to conserve lean tissues (Bauchinger and Biebach 1998). Fast natural

turnover rates of gastrointestinal organs (Bauchinger and McWilliams 2009) should also cause birds to lose lean mass even during short periods of active fasting.

Studies of protein usage in bird migration have been limited by the impossibility of killing a bird twice. QMR analysis represents a fast and accurate means of obtaining repeated body composition measurements of individuals and holds great promise for improving our understanding of lean mass fluctuations in both captive and free-living migratory birds. Despite a small sample size, the recaptured birds in this study provided perhaps the most clear quantitative information on lean body mass changes and I encourage application of QMR technology in field studies with the potential to recapture large numbers of passage migrants.

Lean body mass changes of migrants in NYC indicate that birds using these urban stopover sites will require high protein foods along with the high lipid and carbohydrate foods that are preferred for rapid fattening (Barlein 1998, Karasov and Pinshow 1998). Habitat restoration and management practices should ensure adequate dietary protein sources are available to landbird migrants.

LITERATURE CITED

Åkesson S, Karlsson L, Pettersson J (1992) Body composition and migration strategies: a comparison between robins (*Erithacus rubecula*) from two stop-over sites in Sweden. Vogelwarte 36: 188-195.

Bairlein F (1998) The effect of diet composition on migratory fuelling in Garden Warblers *Sylvia borin*. Journal of Avian Biology 29:546-551.

Bauchinger U, Biebach H (1998) The role of protein during migration in passerine birds. Biol Cons Fauna 102: 299-305.

Bauchinger U, Biebach H (2005) Phenotypic flexibility of skeletal muscles during long distance migration of garden warblers: muscle changes are differentially related to body mass. Annals of the New York Academy of Sciences 1046: 271-281.

Bauchinger U, Wohlmann A, Biebach H (2005) Flexible remodeling of organ size during spring migration of the garden warbler (*Sylvia borin*). Zoology 108: 97-106.

Bauchinger U, McWilliams S (2009) Carbon turnover in tissues of a passerine bird: allometry, isotopic clocks, and phenotypic flexibility in organ size. Physiological and Biochemical Zoology 82: 787-797.

Biebach H, Bauchinger U (2003) Energetic savings by organ adjustment during long migratory flights in Garden Warblers (*Sylvia borin*). Pp. 269-280 in: Avian migration (Berthold P, Gwinner E, Sonnenschein E, eds). Springer-Verlag, Berlin.

Bonter DN, Donovan TM, Brooks EW (2007) Daily mass changes in landbirds during migration stopover on the south shore of Lake Ontario. Auk 124: 122-133.

Carlisle JD, Kaltenecker GS, Swanson DL (2005) Stopover ecology of autumn landbird migrants in the Boise foothills of southwestern Idaho. Condor 107: 244-258.

Carpenter FL, Hixon MA, Beuchat CA, Russell RW, Paton DC (1993) Biphasic mass gain in migrant hummingbirds: body composition changes, torpor, and ecological significance. Ecology 74: 1173-1182.

Cimprich DA, Moore FR (1995) Grey Catbird (*Dumetella carolinensis*). No. 167 in: The birds of North America (Poole A, Gill F, eds). Academy of Natural Sciences, Philadelphia, and American Ornithologists Union, Washington D.C.

Craves JA (2009) A fifteen year study of fall stopover patterns of *Catharus* thrushes at an inland, urban site. Wilson Journal of Ornithology 121: 112-118.

DeCandido R, Allen D (2005) First confirmed nesting of the Pine Warbler (*Dendroica pinus*) in New York City. Kingbird 55: 328-334.

Deerenberg C, Biebach H, Bauchinger U (2002) Spleen size variation during long distance migration in a passerine. Avian Science 2: 217-226.

Dunn EH (2000) Temporal and spatial patterns in daily mass gain of Magnolia Warblers during migratory stopover. Auk 117: 12-21.

Dunn EH (2001) Mass change during migration stopover: a comparison of species groups and sites. Journal of Field Ornithology 72: 419-432.

Falls JB, Kopachena JG (2010) White-throated Sparrow (*Zonotrichia albicolis*). No. 167 in: The birds of North America (Poole A, Gill F, eds). Academy of Natural Sciences, Philadelphia, and American Ornithologists Union, Washington D.C.

Fowle M, Kerlinger P (2001) The New York City Audubon Society guide to finding birds in the metropolitan area. Cornell University Press, New York.

Green AJ (2001) Mass/length residuals: measures of body condition or generators of spurious results? Ecology 82: 1473-1483.

Hume ID, Biebach H (1996) Digestive tract function in the long-distance migratory Garden Warbler, *Sylvia borin*. Journal of Comparative Physiology B 166: 388-395.

Jenni-Eiermann S, Jenni L (1991) Metabolic responses to flight and fasting in night migrating passerines. Journal of Comparative Physiology B 161: 465-474.

Jenni L, Jenni-Eiermann S (1992) Metabolic patterns of feeding, overnight fasted and flying night migrants during autumn migration. Ornis Scandinavica 23:251-259.

Jenni L, Jenni-Eiermann S (1998) Fuel supply and metabolic constraints in migrating birds. Journal of Avian Biology 29: 521-528.

Jenni L, Jenni-Eiermann S, Spina F, Schwabl H (2000) Regulation of protein breakdown and adrenocortical response to stress in birds during migratory flight. American Journal of Physiology and Regulatory Integrative Comparative Physiology 278:1182-1189.

Jones AS, Johnson MS, Nagy TR (2009) Validation of quantitative magnetic resonance for the determination of body composition of mice. International Journal of Body Composition Research 7:67-72.

Jones PW, Donovan TM (1996) Hermit Thrush (*Catharus guttatus*). No. 261 in: The birds of North America. Academy of Natural Sciences, Philadelphia, and American Ornithologists Union, Washington D.C.

Karasov WH, Pinshow B (1998) Changes in lean mass and in organs of nutrient assimilation in a long-distance passerine migrant at a springtime stopover site. Physiological Zoology 71:435-448.

Klaassen M, Biebach H (1994) Energetics of fattening and starvation in the long-distance migratory garden warbler, *Sylvia borin*, during the migratory phase. Journal of Comparative Physiology B 164:362-371.

Klaassen M, Kvist A, Lindström Å (2000) Flight costs and fuel composition of a bird migrating in a wind tunnel. Condor 102:444-451.

Landys-Ciannelli MM, Piersma T, Jukema J (2003) Strategic size changes of internal organs and muscle tissue in the bar-tailed godwit during fat storage on a spring stopover site. Functional Ecology 17:151-159.

Lindström Å, Piersma T (1993) Mass changes in migrating birds: the evidence for fat and protein storage re-examined. Ibis 135:70-87.

Lindström Å, Klaassen M, Kvist A (1999) Variation in energy intake and basal metabolic rate of a bird migrating in a wind tunnel. Functional Ecology 13:352-359.

Lindström Å, Kvist A, Piersma T, Dekinga A, Dietz M (2000) Avian pectoral muscle size rapidly tracks body mass changes during flight, fasting, and fuelling. Journal of Experimental Biology 203:913-919.

Marsh RL (1983) Adaptations of the Gray Catbird *Dumetella carolinensis* to long distance migration: energy stores and substrate concentrations in plasma. Auk 100:170-179.

McGuire LP, CG Guglielmo. Quantitative magnetic resonance: a rapid, noninvasive body composition analysis technique for live and salvaged bats. Journal of Mammalogy, in press.

McWilliams SR, Guglielmo C, Pierce B, Klaassen M (2004) Flying, fasting, and feeding

in birds during migration: a nutritional and physiological ecology perspective. Journal of Avian Biology 35:377-393.

Mehlman DW, Mabey SE, Ewert DN, Duncan C, Abel B, Cimprich D, Sutter RD, Woodrey MS (2005) Conserving stopover sites for forest-dwelling migratory landbirds. Auk 122:1281-1290.

Mittelbach M, Crewdson M (1998) Wild New York: A guide to the wildlife, wild places, and natural phenomena of New York City. Random House, New York.

Moore FR, Gauthreaux SA, Kerlinger P, Simons TR (1995) Habitat requirements during migration: important link in conservation. Pp 121-144 in: Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues (Martin TE, Finch DM, eds). Oxford University Press, New York.

Odum EP, Rogers DT, Hicks DL (1964) Homeostasis of nonfat components of migrating birds. Science 143:1037-1039.

Peig J, Green AJ (2009) New perspectives for estimating body condition fro mass/length data: the scaled index as an alternative method. Oikos 118:1883-1891.

Pennycuick CR (1998) Computer simulation of fat and muscle burn in long-distance bird migration. Journal of Theoretical Biology 191:47-61.

Piersma T (1990) Pre-migratory “fattening” involves more than fat alone. Ringing and Migration 11:113-115.

Piersma T, Jukema J (1990) Budgeting the flight of a long-distance migrant: changes in nutrient reserve levels of bar-tailed godwits at successive spring staging sites. Ardea 78:315-337.

Piersma T, Van Brederode NE (1990) The estimation of fat reserves in coastal waders

before their departure from northwest Africa in spring. Ardea 78:221-236.

Piersma T, Gill Jr RE (1998) Guts don't fly: small digestive organs in obese bar-tailed godwits. Auk 115:196-203.

Piersma T, Gudmundsson GA, Lilliendahl K (1999) Rapid changes in the size of different functional organ and muscle groups during refueling in a long-distance migrating shorebird. Physiological and Biochemical Zoology 72:405-415.

Schwilch R, Grattarola A, Spina F, Jenni L (2002) Protein loss during long distance migratory flight in passerine birds: adaptation and constraint. Journal of Experimental Biology 205:687-695.

Seewagen CL (2008) Lipid content of Nearctic-Neotropical migratory passerines killed during stopovers in a New York City park. Northeastern Naturalist 15:87-96.

Seewagen CL, Slayton EJ (2008) Mass changes of migratory landbirds during stopovers in a New York City park. Wilson Journal of Ornithology 120:296-303.

Seewagen CL, Guglielmo CG (2010). Quantitative magnetic resonance analysis and a morphometric predictive model reveal lean body mass changes in migratin Nearctic-Neotropical passerines. Journal of Comparative Physiology B, *in press*.

Sokal RR, Rohlf FJ (1981) Biometry, 2nd ed. WH Freeman and Company, San Francisco.

Swanson DL, Carlisle HA, Liknes ET (2003) Abundance and richness of Neotropical migrants during stopover at farmstead woodlots and associated habitats in southeastern South Dakota. American Midland Naturalist 149:176-191.

Taicher GZ, Tinsley FC, Reiderman A, Heiman ML (2003) Quantitative magnetic

resonance (QMR) method for bone and whole-body-composition analysis. Analytical and Bioanalytical Chemistry 377:990-1002.

Tankersley Jr R, Orvis K (2003) Modeling the geography of migratory pathways and stopover habitats for Neotropical migratory birds. Conservation Ecology [online] 7:7.

Van Horn MA, Donovan TM (1994) Ovenbird (*Seiurus aurocapillus*). No. 182 in: The birds of North America (Poole A, Gill F, eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists Union, Washington D.C.

van der Meer J, Piersma T (1994) Physiologically inspired regression models for estimating and predicting nutrient stores and their composition in birds. Physiological Zoology 67:305-329.

Warton DI, Wright IJ, Falster DS, Westoby M (2006) Bivariate line-fitting methods for allometry. Biological Reviews 81:259-291.

Wirestam R, Fagerlund T, Rosèn M, Hedenström A (2008) Magnetic resonance imaging for noninvasive analysis of fat storage in migratory birds. Auk 125:965-971.

Table 4.1. Total body mass (TBM), lean body mass (LBM), and fat mass (FM) of migratory landbirds during stopovers in Bronx Park (BP) and Prospect Park (PP), New York City, USA, spring and autumn 2008. TBM measured by digital balance. FM of ovenbirds estimated with a predictive model (see Methods); FM and LBM of other species measured with quantitative magnetic resonance analysis. Values are means ± SE.

	Season	Site	*n*	TBM (g)	LBM (g)	FM (g)
Gray catbird	Autumn	BP	31	40.5 ± 2.8	30.802 ± 2.597	5.435 ± 2.397
Hermit thrush	Autumn	BP	21	31.2 ± 2.0	24.450 ± 1.514	2.763 ± 1.078
Ovenbird	Spring	BP	43	21.0 ± 1.2		3.2 ± 0.7
	Spring	PP	102	20.6 ± 1.7		3.0 ± 1.0
White-throated sparrow	Autumn	BP	39	25.9 ± 2.2	19.719 ± 1.344	2.887 ± 1.260

Table 4.2. Relationships of fat and lean body mass with total body mass in migratory landbirds during autumn 2008 stopovers in Bronx Park, New York City, USA. Slopes (*b*) obtained by major axis type II regression represent the changes in fat and lean body mass (g) per 1 g of total body mass, after controlling for body size.

	Tissue	r^2	*F*	df	*P*	*b*
Gray catbird	Fat	0.21	7.8	1, 29	0.009	0.84
	Lean	0.18	6.7	1, 29	0.017	1.01
Hermit thrush	Fat	0.63	32.2	1, 19	< 0.001	0.50
	Lean	0.27	7.0	1, 19	0.016	0.53
White-throated sparrow	Fat	0.43	27.4	1, 37	< 0.001	0.42
	Lean	0.53	42.2	1, 37	< 0.001	0.48

Table 4.3. Changes in total body mass (TBM; measured by digital balance), fat mass (FM) and lean body mass (LBM; measured with quantitative magnetic resonance) of 4 passerines recaptured during stopovers in Bronx Park, New York City, USA, autumn 2008. All mass data expressed in grams.

Species	First capture			Days	Recapture			Change			
	TBM	FM	LBM		TBM	FM	LBM	ΔTBM	ΔFM	ΔLBM	% as LBM
Hermit thrush	29.5	1.981	23.798	3	31.1	2.766	24.834	1.6	0.785	1.036	65
Hermit thrush	31.9	1.850	25.278	4	33.8	3.705	25.318	1.9	1.856	0.040	2
Hermit thrush	28.4	2.058	21.669	5	31.2	3.904	22.446	2.8	1.846	0.777	28
Ovenbird	18.3	1.068	15.149	8	22.5	3.835	16.982	4.2	2.767	1.833	44

CHAPTER V

EFFECTS OF FAT AND LEAN BODY MASS ON LANDBIRD STOPOVER DURATIONS IN AN URBAN HABITAT: A PILOT STUDY[1]

INTRODUCTION

Migrating landbirds require several stopovers for rest and refueling, as most are incapable of completing their migration in a single flight. Time and energy spent during stopover periods greatly exceeds that spent aloft (Wikelski et al. 2003, Bowlin et al. 2005), and behaviour of birds at stopover sites can greatly influence their overall migration success. Factors that govern a bird's decision to terminate a stopover and begin the next flight have received much attention, particularly through development of theoretical models of optimal migration strategies (Alerstam and Hedenström 1998, Houston 1998). There is evidence that fuel stores, refueling rate, distance from final destination, date, predation risk, and weather conditions can individually, or in some combination, influence a bird's length of stay at a given stopover site (Wang and Moore 1997, Åkesson and Hedenström 2000, Danhardt and Lindström 2001, Dierschke and Delingat 2001, Schaub et al. 2008).

Field studies of the effects of intrinsic and extrinsic factors on stopover duration are hampered by the difficulty of knowing when birds arrive at, and depart from, the site of interest. Several studies have measured stopover duration using mark-recapture data, while assuming birds were marked upon arrival and final recapture occurred on their actual departure date (e.g., Cherry 1982, Wang and Moore 1997, Morris and Glasgow 2001). The latter assumption can be especially tenuous, as migrants may learn to avoid

[1] A version of this chapter has been published (Seewagen and Guglielmo 2010) and is presented here with permission from the Wilson Ornithological Society.

mist nets (MacArthur and MacArthur 1974) or move beyond the coverage area within the stopover site (Chernetsov and Mukhin 2006, Tsvey et al. 2007). This method also relies on the condition and behaviour of the small proportion of birds that are recaptured to represent the majority, when recaptures may be biased towards individuals in poor condition that remain at the site for a relatively long time (Guglielmo et al. 2005, Morris et al. 2005, Hays 2008). More recently, survival analyses and other probabilistic models have been used to relax these assumptions and improve accuracy of stopover duration estimates based on mark-recapture data (Schaub et al. 2001, 2008), although large sample sizes are generally needed (Schaub 2006). Radio tracking offers another approach for measuring stopover duration that does not rely on recaptures and allows knowing departure date with near certainty (Chernetsov and Mukhin 2006, Tsvey et al. 2007).

Examining the effect of energetic condition on stopover duration is complicated by the need for accurate, non-lethal measurements of body composition. Commonly used condition indices (e.g., body mass, size-corrected body mass, visual fat scores) can potentially provide reliable estimates of fat content (Conway et al. 1994, Spengler et al. 1995, Chapter II). However, their accuracy may be species-specific (Skagen et al. 1993, Spengler et al. 1995, Chapter II) or weakened by inter-observer variation (Krementz and Pendleton 1990), and they do not provide separate, direct measures of fat and lean body mass. Quantitative magnetic resonance analysis (QMR; Taicher et al. 2003, Tinsley et al. 2004) in contrast provides accurate, objective, and direct measures of the fat and lean body mass of small birds (Guglielmo, Gerson, McGuire, and Seewagen, unpublished data).

I attached radio transmitters on 11 migrant songbirds in New York City during autumn 2008 in a pilot study to test the feasibility of radio tracking birds in an urban setting before proceeding with the larger-scale telemetry efforts presented in Chapter VI. I used a QMR body composition analyzer on all captured migrants for a concurrent study of body composition dynamics during stopover refueling (Chapter IV). The stopover duration and body composition data obtained by radiotelemetry and QMR, respectively, afforded an additional opportunity to examine relationships between these variables. I coupled the telemetry and QMR data to examine if arrival fat and lean body mass affected the stopover durations of these 11 migrants in an urban habitat.

METHODS

Study site and data collection

I captured birds during autumn 2008 on the grounds of the Bronx Zoo. The Bronx Zoo is 107 ha and within Bronx Park in Bronx County, New York, USA. My study site was a 4.9-ha fragment of riparian forest on the eastern edge of the zoo that does not contain exhibits and is not open to visitors (40° 85' N, 73° 87' W). Red oak (*Quercus rubra*), sweet gum (*Liquidambar styraciflua*), swamp dogwood (*Cornus foemina*), and willows (*Salix* spp.) are the dominant tree species in the area. Previous research has suggested this site offers suitable refueling conditions for landbird migrants (Seewagen and Slayton 2008, Chapter III).

Birds were captured in mist nets from sunrise until ~12:00 EST during 4 September to 22 October. Captured birds were marked with a U.S. Geological Survey aluminum leg band, measured (unflattened wing length to 1 mm), and weighed on a

digital balance to 0.1 g. Approximately 75 µl of blood was collected by brachial veinipuncture for a separate study (Chapter III). Fat and lean body mass were then measured to 0.001g by QMR analysis as described in Chapter IV.

Radiotelemetry

I radio-tagged each Swainson's thrush *(Catharus ustulatus)*, hermit thrush (*C. guttatus*), and ovenbird (*Seiurus aurocapilla*) captured beginning 3 October until all 11 transmitters were deployed. These species were used because they are relatively common migrants in the area, body masses are amenable to radiotelemetry, and they are focal species of other chapters. The 0.5-g transmitters (A2415, Advanced Telemetry Systems, Isanti, MN, USA) were affixed after QMR scanning with eyelash adhesive directly to a cleared area of skin in the interscapular region (adapted from Raim 1978). Birds were held in bags for ~15 min to allow the adhesive to dry and released within 50 m of where originally captured.

I could not be certain birds were captured and marked upon arrival. Eight of 11 birds were marked on days when migrant capture rates were high (~double) relative to the 2 previous days. This increased my confidence these individuals were new arrivals and marked during their first day at the stopover site (*sensu* Tsvey et al. 2007). However, I use the term 'minimum stopover duration' hereafter because of this uncertainty.

I checked for presence/absence daily at sunrise, noon, and sunset using a handheld Yagi antenna and receiver (R4500S, Advanced Telemetry Systems, Isanti, MN, USA) from within the study site. I searched for birds from other points throughout the zoo including roofs of two three-story buildings if I initially failed to detect a signal from

within the study site. I assumed birds had left the area permanently and resumed migration if they were undetected for at least 4 consecutive days. I considered a stopover of 1 day as the initial capture of a bird at the site in the morning and departure any time that night.

Statistical Analyses

I used standardized residuals from linear regressions of lean body mass and wing length to correct lean body mass for body size variation. I could not adjust fat mass in the same manner because fat mass was not significantly related to wing length. I instead divided fat mass by total body mass and arcsine-root transformed the proportions (Zar 1999, Gotelli and Ellison 2004).

I used backwards selection multiple regression with adjusted fat and lean body mass as predictor variables, and number of days of stopover as the response variable, to examine the effect of body composition on stopover duration. Collinearity did not occur, as fat and lean body mass were not significantly correlated. I performed the analyses on ovenbird data alone and on data from all three species combined.

Age and gender were not considered because sample sizes were small and not all birds could be confidently assigned to age or sex classes. All variables met normality assumptions. I conducted tests with SPSS 16.0 and interpreted results as significant when $P < 0.05$. Mean (± SD) values are reported.

RESULTS

I radio-tagged two Swainson's thrushes, two hermit thrushes, and seven ovenbirds. Swainson's thrushes were marked on 2 and 6 October, and hermit thrushes were marked on 10 and 11 October. Four ovenbirds were marked on 3 October and three were marked on 6 October.

Minimum stopover durations ranged from 1 to 14 days (Table 5.1). Three individuals departed within 1 day and the remainder stayed for at least 2 days. Initial fat content ranged from 6 to 8% of total body mass in Swainson's thrushes, from 5 to 12% in Hermit thrushes, and from 6 to 18% in ovenbirds. An ovenbird was recaptured on the eighth day of its 14 day stopover; total body mass (measured by digital balance) increased 4.2 g and fat and lean body mass (measured by QMR) respectively increased 2.767 g and 1.833 g, as reported in Chapter IV.

The initial fat loads of birds that stayed at the site for only 1-2 days ($n = 5$) averaged 14 ± 3% of total body mass, whereas the initial fat loads of birds that stayed for the longest periods (7, 8, and 14 days; $n = 3$) averaged 6 ± 0.5% of total body mass. Ovenbird stopover duration was unrelated to lean body mass ($r^2 = 0.02$, $F_{2, 4} = 0.36$, $P = 0.58$), and significantly and negatively related to fat mass ($r^2 = 0.74$, $F_{1, 5} = 13.95$, $P = 0.013$). The same relationships were found when data from all three species were combined to increase sample sizes (lean: $r^2 = 0.03$, $F_{2, 8} = 0.00$, $P = 0.98$; fat: $r^2 = 0.56$, $F_{1, 9} = 11.31$, $P = 0.008$; Fig. 5.1). The relationship between fat and stopover duration appeared non-linear, and I explored the fit of an exponential model to the data *a posteriori*. The exponential model was also highly significant ($r^2 = 0.71$, $F_{1, 9} = 22.08$, $P = 0.001$; Fig. 5.1).

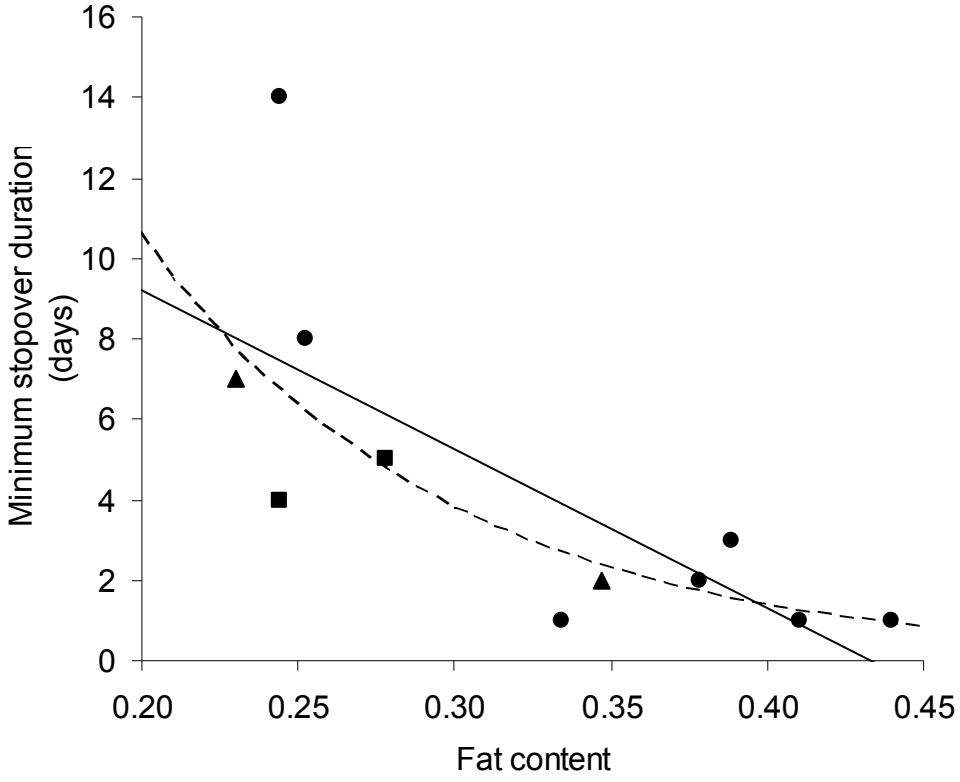

Figure 5.1. Relationship between arrival fat content (arcsine-root transformed g fat/g total body mass) and minimum stopover duration of Swainson's thrushes (squares), hermit thrushes (triangles), and ovenbirds (circles) captured during autumn migration in New York City, USA. Solid and dashed lines represent linear ($r^2 = 0.56$, $F_{1, 9} = 11.31$, $P = 0.008$) and exponential ($r^2 = 0.71$, $F_{1, 9} = 22.08$, $P = 0.001$) models, respectively.

DISCUSSION

To my knowledge this is the first combination of magnetic resonance technology and radiotelemetry to examine the influence of both fat and lean body mass on stopover duration. I believe this is also the first description of autumn stopover durations of migrants within a major urban center.

Fat mass upon presumed arrival date appeared to strongly influence how long birds remained at the stopover site. This is consistent with other findings that lean birds stop over longer than fatter birds (Cherry 1982, Loria and Moore 1990, Wang and Moore 1997, Matthews 2008; but see Safriel and Lavee 1988, Salewski and Schaub 2007, Chapter VI). The arrival fat content of individuals that stayed for only 1 day was at least 11% of total body mass, whereas all individuals with fat content < 6% of total body mass remained for no fewer than 4 days, suggesting a possible threshold fat level for departure. However, how much additional fat birds acquired between capture and departure is unknown.

Lean tissues can contribute significantly to total body mass dynamics during stopovers (e.g., Karasov and Pinshow 1998, Chapter IV). Thus lean body mass upon arrival should influence stopover duration when refueling includes the deposition of lean tissues, as shown in Chapter IV. Yet in this study I did not find any relationship between lean body mass and minimum stopover duration. It is possible a type II error occurred due to the small sample size of only eleven birds. However, the findings of Fusani et al. (2009) also suggest that lean mass does not influence departure decisions of passerine migrants. Further study on the relationship between lean body mass and stopover duration is needed.

Fuel load is not the only variable that can influence stopover duration; weather, predation risk, and date are also factors that possibly govern a bird's decision to depart a stopover site. The small sample size of 11 birds prohibited including additional predictor variables in the analyses and I cannot assess any effect they may have had on stopover duration. However, the birds were marked on 5 days over a span of only 9 days; thus, they probably experienced similar predation risk and temporal pressure, and were exposed to comparable weather conditions. Arrival body composition likely differed among the individuals we studied more so than any of these potential extrinsic influences.

The recaptured ovenbird may illustrate how multiple variables can affect stopover duration. This bird appeared to have stored sufficient fat to resume migration by its eighth stopover day, yet it remained at the site for 6 additional days. Overnight wind direction following recapture was primarily from the south until the night the bird departed when winds came from the north, the preferred direction of southbound passerines (Gauthreaux 1991). It is possible this bird was energetically prepared for departure by the eighth day but waited 6 additional days for more favorable overnight flying conditions. Six of the other birds similarly departed on nights with northern winds; the remaining four departed during eastern winds.

My sample size was small, but arrival fat mass had a clear and strong effect on time birds remained at the stopover site. Similar relationships between stopover duration and some measure of energetic condition have been documented previously (Cherry 1982, Loria and Moore 1990, Wang and Moore 1997, Matthews 2008), but the contributions of fat and lean mass were not addressed individually. Quantitative magnetic resonance scanning allowed me to separately examine how each tissue affected stopover

duration. Arrival fat mass at the study site affected migrants' decisions to leave whereas lean body mass did not. Thus, the conditions for increasing or maintaining fat stores provided by this site and possibly other similar urban habitats can affect the migration timing of birds using them. My results demonstrate quantitative magnetic resonance analysis can be useful under field conditions, and that combining it with telemetry and other approaches will improve our ability to understand the stopover biology of birds.

LITERATURE CITED

Åkesson S, Hedenström A (2000) Wind selectivity of migratory flight departures in birds. Behavioral Ecology and Sociobiology 47:140-144.

Alerstam T, Hedenström A (1998) The development of bird migration theory. Journal of Avian Biology 29:343–369.

Bowlin MS, Cochran WW, Wikelski MC (2005) Biotelemetry of New World thrushes during migration: physiology, energetics and orientation in the wild. Integrative and Comparative Biology 45:295-304.

Chernetsov N, Mukhin A (2006) Spatial behavior of European Robins during migratory stopovers: a telemetry study. Wilson Bulletin 118:364-373.

Cherry JD (1982) Fat deposition and length of stopover of migrant White-crowned Sparrows. Auk 99:725-732.

Conway CJ, Eddleman WR, Simpson KL (1994) Evaluation of lipid indices of the Wood Thrush. Condor 96:783-790.

Danhardt J, Lindström A (2001) Optimal departure decisions of songbirds from an experimental stopover site and the significance of weather. Animal Behavior 62:235-243.

Dierschke V, Delingat J (2001) Stopover behaviour and departure decision of Northern Wheatears, *Oenanthe oenanthe*, facing different onward non-stop flight distances. Behavioral Ecology and Sociobiology 50:535-545.

Fusani L, Cardinale M, Carere C, Goymann W (2009) Stopover decision during migration: physiological conditions predict nocturnal restlessness in wild passerines. Biology Letters 5:302-305.

Gauthreaux Jr. SA (1991) The flight behavior of migrating birds in changing wind fields: radar and visual analyses. American Zoologist 31:187-204.

Gotelli NJ, Ellison AM (2004) A primer of ecological statistics. Sinauer Associates, Sunderland.

Guglielmo CG, Cerasale DJ, Eldermire C (2005) A field validation of plasma metabolite profiling to assess refueling performance of migratory birds. Physiological and Biochemical Zoology 78:116-125.

Hays QR (2008) Stopover behavior and refueling physiology in relation to migration distance in Wilson's Warblers (*Wilsonia pusilla*). Thesis. University of Western Ontario, London, ON.

Houston AI (1998) Models of avian optimal migration: state, time and predation. Journal of Avian Biology 29:395-404.

Karasov WH, Pinshow B (1998) Changes in lean mass and in organs of nutrient assimilation in a long-distance passerine migrant at a springtime stopover site. Physiological Zoology 71:435-448.

Krementz DG, Pendleton GW (1990) Fat scoring: sources of variability. Condor 92:500-507.

Loria DE, Moore FR (1990) Energy demands of migration on Red-eyed Vireos, *Vireo olivaceus*. Behavioral Ecology 1:24-35.

MacArthur RH, MacArthur AT (1974) On the use of mist nets for population studies of birds. Proceedings of the National Academy of Sciences 71:3230- 3233.

Matthews SN (2008) Stopover habitat utilization by migratory landbirds within urbanizing landscapes of central Ohio. Dissertation. Ohio State University, Columbus, OH.

Morris SR, Glasgow JL (2001) Comparison of spring and fall migration of American Redstarts on Appledore Island, Maine. Wilson Bulletin 113:202-210.

Morris SR, Liebner DA, Larracuente AM, Escamilla EM, Sheets HD (2005) Multiple day constancy as an alternative to pooling for estimating mark-recapture stopover length in Nearctic-neotropical migrant landbirds. Auk 122:319-328.

Raim A (1978) A radio transmitter attachment for small passerine birds. Bird-Banding 49:326-332.

Safriel UN, Lavee D (1988) Weight changes of cross-desert migrants at an oasis — do energetic considerations alone determine the length of stopover? Oecologia 76:611-619.

Salewski V, Schaub M (2007) Stopover duration of Palearctic passerine migrants in the western Sahara – independent of fat stores? Ibis 149:223-236.

Schaub M (2006) How to study departure decisions of migrants from stopover sites using capture-recapture data. Acta Zoologica Sinica 52:602-605.

Schaub M, Jenni L, Bairlein F (2008) Fuel stores, fuel accumulation, and the decision to depart from a migration stopover site. Behavioral Ecology 19:657-666.

Schaub M, Pradel R, Jenni L, Lebreton J (2001) Migrating birds stop over longer than usually thought: an improved capture-recapture analysis. Ecology 82:852-859.

Seewagen CL, Slayton EJ (2008) Mass changes of migratory landbirds during stopovers in a New York City park. Wilson Journal of Ornithology 120:296-303.

Seewagen CL, Guglielmo CG (2010) Effects of fat and lean body mass on migratory landbird stopover duration. Wilson Journal of Ornithology 122:82-87.

Skagen SK, Knopf FL, Cade BS (1993) Estimation of lipids and lean mass of migrating sandpipers. Condor 95:944-956.

Spengler T J, LeBerg PL, Barrow Jr WC (1995) Comparison of condition indices in migratory passerines at a stopover site in coastal Louisiana. Condor 97:438-444.

Taicher GZ, Tinsley FC, Reiderman A, Heiman ML (2003) Quantitative magnetic resonance (QMR) method for bone and whole-body-composition analysis. Analytical and Bioanalytical Chemistry 377:990-1002.

Tinsley FC, Taicher GZ, Heiman ML (2004) Evaluation of a quantitative magnetic resonance method for mouse whole body composition analysis. Obesity Research 12:150-160.

Tsvey A, Bulyuk VN, Kosarev V (2007) Influence of body condition and weather on departures of first-year European Robins, *Erithacus rubecula*, from an autumn migratory stopover site. Behavioral Ecology and Sociobiology 61:1665-1674.

Wang Y, Moore FR (1997) Spring stopover of intercontinental migratory thrushes along the northern coast of the Gulf of Mexico. Auk 114:263-278.

Wikelski, M., E. M. Tarlow, A. Raim, R. H. Diehl, R. P. Larkin, and G. H. Visser. 2003. Costs of migration in free-flying songbirds. Nature 423:704.

Zar JH (1999) Biostatistical analysis, 4th ed. Prentice Hall, Englewood Cliffs.

Table 5.1. Means ± SD and ranges of total body mass, fat mass, lean body mass, and minimum stopover durations of three species of migratory landbirds radiotracked during autumn stopovers in New York City, USA.

Species	*n*	Total body mass (g)	Fat mass (g)	Lean body mass (g)	Stopover duration (days)
Swainson's thrush	2	27.3, 30.1	1.700, 2.410	22.760, 26.119	4, 5
Hermit thrush	2	30.2, 34.6	1.570, 4.000	27.103, 29.089	2, 7
Ovenbird	7	20.0 ± 1.3 18.3-21.7	2.461 ± 1.069 1.068-3.911	17.009 ± 0.795 15.713-18.145	4.3 ± 5.0 1-14

CHAPTER VI

SPATIOTEMPORAL BEHAVIOURS OF PASSERINE MIGRANTS AT AN URBAN STOPOVER SITE: MOVEMENT PATTERNS, STOPOVER DURATIONS, AND THE INFLUENCE OF ARRIVAL CONDITION[1]

INTRODUCTION

Migration for most landbird species involves long-distance nocturnal flights followed by stopover periods when energy stores are replenished before continuing towards their ultimate destination. More time and energy is spent during stopovers than during flight (Wikelski et al. 2003, Bowlin et al. 2005) and the behaviour of birds in stopover habitats significantly influences the economy, duration, and overall success of their migration. This is particularly so during spring when males face pressure to arrive on their breeding grounds early enough to secure a territory and the energetic condition of both sexes upon arrival can affect reproductive performance (Sandberg and Moore 1996, Kokko 1999, Smith and Moore 2003).

Migrants are expected to select stopover habitats that allow them to refuel with maximum efficiency and remain close to their migratory schedules (Lindström and Alerstam 1992). Upon landfall birds must familiarize themselves with novel habitat and assess food availability, competition, and predation risk before selecting a particular area to occupy (Chernetsov 2006). This early phase of stopover is referred to as 'search and settling' and may include behavioural as well as physiological adjustments (Alerstam and Hedenström 1998, Karasov and Pinshow 2000). Distribution patterns suggest landbird

[1] A version of this chapter has been published (Seewagen et al. 2010) and is presented here with permission from Elsevier.

migrants favor particular habitat characteristics (e.g., Rodewald and Brittingham 2004, 2007; Strode 2009) and such preferences usually reflect differences in refueling opportunities (Simons et al. 2000, Buler et al. 2007, Tietz and Johnson 2007, Ktitorov et al. 2008, Cerasale and Guglielmo 2010).

Widespread anthropogenic alterations to the North American landscape have degraded and reduced the amount of habitat available for use as stopover sites by Nearctic-Neotropical migrants (McCann et al. 1993, Mehlman et al. 2005, Carlisle et al. 2009). Many species' migration routes follow the Atlantic or Pacific coasts where the largest human population centers of the United States are located and urbanization is a predominant land cover type. Migrants encountering metropolitan areas and in need of stopover habitat will usually be limited to small woodlots and forest fragments within city parks. The resulting occurrence of migrants in urban habitats, often at high densities, has been documented and recognized for quite some time (Chapman 1910, Griscom 1923, Brawn and Stotz 2001, Fowle and Kerlinger 2001). Yet, the potential value of urban habitats to migrants has been largely disregarded until recently (Matthews 2008, Pennington et al. 2008, Seewagen 2008, Seewagen and Slayton 2008) and knowledge of migratory bird ecology and behaviour in such places remains severely limited.

Radio telemetry studies in non-urban areas have shown migrant songbird behaviour to often consist of exploratory, linear movements upon arrival at a new stopover site, followed by more aggregated movements on subsequent days presumably after a suitable microhabitat has been encountered (Chernetsov 2005, Buler 2006, Chernetsov and Mukhin 2006, Paxton et al. 2008). It is unknown whether the movement patterns of migrants in urban stopover sites fit this trend. If urban habitat quality is

marginal and levels of disturbance are great, birds may move widely within the site without ever settling, and depart when the energetic and temporal costs of the stopover begin to exceed the benefits.

I examined the fine-scale movements of a common Neotropical migrant passerine, the ovenbird (*Seiurus aurocapillus*), within an urban stopover site to learn whether birds exhibited the search and settling behaviour characteristic of birds studied in less developed and disturbed, non-urban settings. I additionally measured stopover durations and temporary home range sizes, and how arrival condition and season influenced each of these metrics. Taken together, these investigations elucidate how landbird migrants are utilizing urban habitats as stopover sites in space and time. Detailed knowledge of migrant habitat use and stopover behaviour is needed for effective stopover site conservation and management in rural and urban areas alike (Petit 2000, Mehlman et al. 2005, Chernetsov 2006, Rodewald and Brittingham 2007, Pennington et al. 2008, Carlisle et al. 2009).

METHODS

Study species

The ovenbird is a common forest-dwelling passerine that breeds across much of Canada and the eastern United States, and over-winters throughout Central America and the Caribbean islands. Ovenbirds are most often found on the forest floor where they forage for insects in the leaf litter (Van Horn and Donovan 1994). I selected ovenbirds as a focal species because they are long-distance migrants that do not nest or over-winter in New York City (Van Horn and Donovan 1994, DeCandido and Allen 2005), they are common

enough during migration to provide adequate sample sizes, and their body mass is sufficient for carrying radio transmitters (Bayne and Hobson 2001, Brown 2006, Buler 2006). In addition, ovenbird movement patterns in a non-urban stopover site have been described (Buler 2006) which provides useful context in which to interpret my findings.

Study site

I studied ovenbird stopover behaviour in New York City's Prospect Park (Fig. 6.1). New York City is the United States' largest city (US Census Bureau 2010) and is located at the nexus of four major migration routes (southeastern U.S. route, circum-Gulf route, trans-Gulf route, and Caribbean island-western North Atlantic route) that over 100 species of birds follow each year (Rappole et al. 2000). Prospect Park is a 213 ha public park in the center of the borough of Brooklyn (Kings County). Brooklyn has a human population of approximately 2.6 million and a total land area of 183 km^2, equaling a population density of 13,970 people/km^2 (US Census Bureau 2010). More than 6 million people visit Prospect Park each year (Wells 1998). The park is a highly isolated habitat island surrounded by heavy urbanization and contains the last remaining eastern deciduous woodland in Brooklyn. Aside from neighboring Greenwood Cemetery, the nearest significant greenspace (>100 ha) is approximately 7 km northeast in the borough of Queens. Exceptional concentrations of landbird migrants routinely occur in Prospect Park due to its geographic position and expansive inhospitable surroundings (Wells 1998, Fowle and Kerlinger 2001).

Prospect Park is a mosaic of landscaped meadows and lawns, athletic fields, man-made water-bodies, and remaining natural forests and wetlands. Approximately half

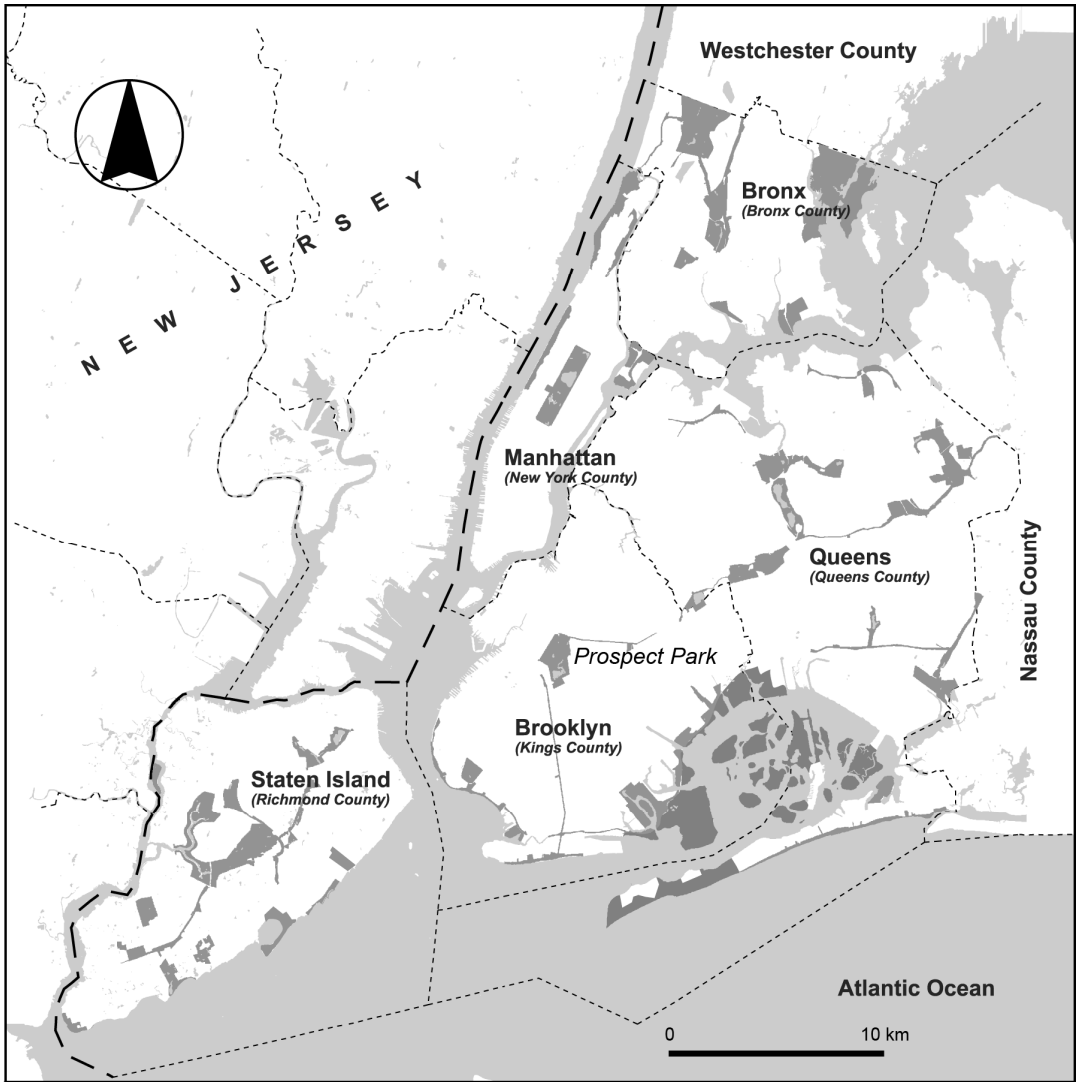

Figure 6.1. Natural areas (>100 ha) remaining within New York City, USA (indicated in dark gray). New York City includes Brooklyn, Bronx, Manhattan, Queens, and Staten Island. Ovenbird stopover behavior was studied in Prospect Park, Brooklyn. Reproduced with permission from DeCandido et al. (2004: p.244).

of the park is mature deciduous forest (Wells 1998). I captured birds in 'The Ravine' section (40° 39' 49" N, -73° -58' -12" W) of the ~100 ha forest in the center of the park that represents the majority of the park's wooded area (Mittelbach and Crewdson 1998). Its northern and southern edges are bordered by a two-lane road (closed to public vehicular traffic at most times of day) and the eastern and western edges are bordered by a long recreational field and a lake, respectively. The forest is heavily fragmented by meandering, paved walking trails ~5m wide. The tree community is dominated by black cherry (*Prunus serotina*), red oak (*Quercus rubra*), tulip poplar (*Liriodendron tulipifera*), and willows (*Salix* spp.), and the woody understory is primarily composed of arrowwood viburnum (*Viburnum dentatum*) and shadbush (*Amelanchier humilis*). The area is actively managed to control the spread of exotic invasive plants and promote the growth of native flora.

Capture and radio-tagging

Spring and autumn migrants were passively captured in 8-10 mist nets daily during 5-18 May and 9 September-1 October, 2009. These dates correspond with the peak spring and autumn passage periods of ovenbirds through NYC. Nets were opened at sunrise and checked for birds every 20 min for approximately three hours. Captured ovenbirds were banded with USGS aluminum leg bands, weighed to 0.1g on a digital balance, measured (unflattened wing length to 1mm), assigned to age and sex when possible, and fat-scored on a 6-point scale (Moore and Kerlinger 1987, Chapter II). I attempted to increase the likelihood radio-tracking began on a bird's first stopover day by radio-tagging birds on mornings when it appeared a new wave of migrants had arrived, following one or two

previous mornings when relatively few migrants were present in the park (Chernetsov and Muhkin 2006). Nevertheless, I could not be certain birds were tagged on the morning of arrival. Measures of stopover duration may be conservative and I hereafter use the term "minimum stopover duration" (MSD) because of the uncertainty.

Birds were radio-tagged by trimming a few feathers in the interscapular region and affixing the transmitter (model A2426, Advanced telemetry Systems, MN, USA) with eyelash adhesive (American International Industries, CA, USA) directly to the exposed skin (adapted from Raim 1978). Birds were wrapped in a cotton bag for ~10 min while the adhesive dried and then released at their capture location. Transmitters had a battery life of 21 d and a measured range of ~100 m in the forested study area. Transmitters weighed < 3% of each bird's body mass (Gaunt et al. 1997) and I assumed they did not adversely affect the birds' condition or mobility (Brigham 1989, Sykes et al. 1990, Naef-Daenzer 1994, Rae et al. 2009). Direct observations of radio-tagged birds throughout stopovers provided no indication the transmitters were altering their behaviour. Radio-tagged birds were commonly observed foraging normally and no birds were seen attempting to pull off their transmitter. Other telemetry studies have also reported no noticeable adverse reactions of ovenbirds to radio transmitters (Brown 2006, Buler 2006).

Radio tracking

Birds were located every 45-60 min following release until twilight using a Yagi antenna connected to a R-1000 (Communications Specialists, CA) or R4500S (Advanced Telemetry Systems, MN) receiver. Birds that were still present on subsequent days were

located every 45-60 min between sunrise and twilight. This sampling rate was chosen to allow birds ample time to move from one end of their home range to another and increase the independence of observations (White and Garrott 1990, Chernetsov and Mukhin 2006).

Bird positions were determined by homing (White and Garrott 1990, Bayne and Hobson 2001, Paxton et al. 2008) and birds were approached to within an estimated 10 m to avoid disturbance from the observer (Paxton et al. 2008). It was determined a bird was ~10 m away based on visual observation or signal strength. When a signal could not be detected from a bird's last known position, observers expanded outward at approximately 50 m intervals on foot or by bicycle until either the bird was found or it could be concluded the bird was no longer present anywhere in the park. Birds were assumed to have resumed migration if they were undetected for at least two consecutive days after last contact. No birds ever reappeared following a day of no detection.

Bird locations were recorded with a handheld Global Positioning System (model GPS 12, Garmin, KS) at an average accuracy of ±9 m during spring and ±10 m during autumn. During spring, coordinates were recorded as degrees, minutes, and seconds. It was later decided higher resolution coordinates would be more appropriate for the small-scale movements of ovenbirds observed during spring, and coordinates during autumn were therefore recorded in UTM format.

Movement characteristics and home range estimation

I calculated three movement parameters to characterize daily spatial behaviour: movement rate, displacement distance, and a linearity index (Chernetsov 2005, Buler

2006, Chernetsov and Mukhin 2006, Paxton et al. 2008). Movement rate (m hr^{-1}) was calculated as the sum of the distances between each successive location in a day divided by total tracking time. Displacement (m) was calculated as the linear distance between a bird's locations at sunrise (or release) and twilight. The linearity index was calculated as displacement distance divided by the sum of all distances between successive locations within a day. The linearity index is a measure of aggregation, with values ranging from 0 (indicating clustered movements) to 1 (indicating linear movements). Distances between points were measured using the Hawth's Tools extension (Beyer 2004) in ArcMap version 9.2 (ESRI, Redlands, CA).

I used Hawth's Tools to measure fixed kernel home range sizes of birds tracked for at least two days (and with $\geq$ 18 known locations), with least squares cross validation smoothing parameters (Seaman et al. 1999, Borger et al. 2006) calculated with Animal Movement version 2.0 (Hooge and Eichenlaub 2000) in ArcView version 3.2 (ESRI, Redlands, CA). Home range estimates for birds with more sampling locations were not inflated, as I found no significant effect of location sample size on home range area among birds that stayed two or more days. I report fixed kernel home ranges measured with 50, 90, and 95% isopleths because the 95% isopleth is most commonly used, but it may overestimate home range size and more conservative isopleths of 50-90% have been recommended (Borger et al. 2006). Lastly, I used the site fidelity test in Animal Movement 2.0 to determine whether birds (tracked at least two days) occupied defined areas or moved at random. The site fidelity test uses a Monte Carlo simulation to compare the parameters of a bird's actual movements to 1,000 randomly generated paths, starting from the bird's first location.

Statistical analyses

Non-normal data were $\log_{10}$ +1 transformed to achieve normality and non-parametric tests were used when transformations failed to normalize data. I used SPSS version 17 (SPSS Inc., Chicago, IL) for all analyses and accepted significance at $P \leq 0.05$. Age and sex were not considered because total sample sizes were small, spring birds could not be sexed with sufficient confidence, and exploratory analyses revealed no significant differences during autumn between juvenile and adult movement parameters, MSD, or home range sizes. All data are reported as means ± SE.

I used multivariate analysis of variance (MANOVA) to examine daily changes in movement parameters, with days since radio-tagging (stopover day) as the independent variable and movement rate, displacement distance, and the linearity index as response variables. When overall differences among days were significant, I ran a univariate analysis of variance (ANOVA) with Tukey's HSD post-hoc tests for each individual movement parameter. Movement data collected after the fourth day of a stopover were combined into the category 5+ because few birds stayed at the site more than five days in either season. First-day movement parameters of birds that stayed at the stopover site for only one day were compared to those that stayed multiple days with MANOVA, with stopover length (i.e., one day or more than one day) as the grouping variable and first-day movement rate, displacement distance, and linearity index as dependent variables.

Spring and autumn MSDs were non-normal and compared with a Mann-Whitney *U*-test. MSD was measured as days elapsed between the morning of initial capture and the evening of last contact. Spring and autumn 95% fixed kernel home range sizes were compared with a Student's *t*-test. Fat mass upon capture was estimated with a predictive

model (Chapter II) and compared between spring and autumn birds with a Welch-corrected *t*-test. Differences in GPS format resolution during spring and autumn precluded direct seasonal comparisons of the more fine-scale movement parameters. I used simple linear regression or Spearman rank correlation to examine the relationship between arrival fat mass and first-day movement parameters, total home range size (95%), and MSD.

RESULTS

Spring

I radio-tagged 33 ovenbirds during spring. The first bird was tagged 5 May and the last tagged bird left the site 21 May. Transmitters fell off six birds before departure, resulting in incomplete movement data and indeterminate stopover durations for these individuals. In addition, first-day movement data from two birds were omitted due to poor GPS accuracy, providing a final sample size of 25 individuals for the first-day movement parameter analyses.

MSD averaged 3.0 ± 0.5 d and ranged 1-10 d. (n = 27). Thirteen birds (48%) departed the first night following their capture. Most birds remained close to where they were captured and released throughout their stopover. Maximum linear distances birds traveled from their release point averaged 236 ± 30 m (range = 47-715 m). Ovenbirds did not spend time in non-forested areas, but birds that moved far from their release location usually crossed park roads or the large recreational field bordering the study site in doing so.

Overall differences in movement parameters among days were significant (Wilk's $\lambda = 0.62$, $F_{12, 156} = 2.63$, $P = 0.003$; Fig. 6.2). There were no daily differences in movement rate ($F_{4, 61} = 0.67$, $P = 0.62$), whereas there were significant daily differences in linearity ($F_{4, 61} = 2.97$, $P = 0.026$), and daily differences in displacement distance that approached significance ($F_{4, 61} = 2.35$, $P = 0.06$). Displacement distances and linearity indices beyond the fourth stopover day were significantly lower than on previous days (Tukey's HSD post-hoc tests; displacement: $P = 0.038$; linearity index: $P = 0.024$; Fig. 6.2). During the first stopover day, the movement parameters of birds that departed that night were not significantly different from those of birds that stayed additional days (Wilk's $\lambda = 0.77$, $F_{3, 21} = 2.05$, $P = 0.14$).

Fifteen birds provided enough locations for home range estimates. Home range size differed greatly depending on the isopleth (Table 6.1) and individual variation was high (range = 1.0-13.3 ha at 95%). On average, ovenbirds occupied 4.8 ± 1.1 ha when measured with the commonly used 95% isopleth. Site fidelity tests suggested 53% of these birds exhibited non-random, area-restricted movements (all $P < 0.02$).

Few ovenbirds ($n = 2$) were considered lean (<10% fat) upon capture. Estimated fat stores averaged 3.1 ± 0.1 g and most birds' fat stores represented 14-20 % (mean = 14.8 ± 0.5%) of their total body mass. There was no significant relationship between fat mass and first-day movement rate ($r^2 = 0.12$, $F_{1, 23} = 3.14$, $P = 0.09$), displacement distance ($r^2 = 0.00$, $F_{1, 23} = 0.05$, $P = 0.82$) or linearity ($r^2 = 0.00$, $F_{1, 23} = 0.05$, $P = 0.83$) on the day of arrival, total home range size ($r^2 = 0.00$, $F_{1, 13} = 0.00$, $P = 0.97$), or MSD ($r_S = -0.01$, $P = 0.96$).

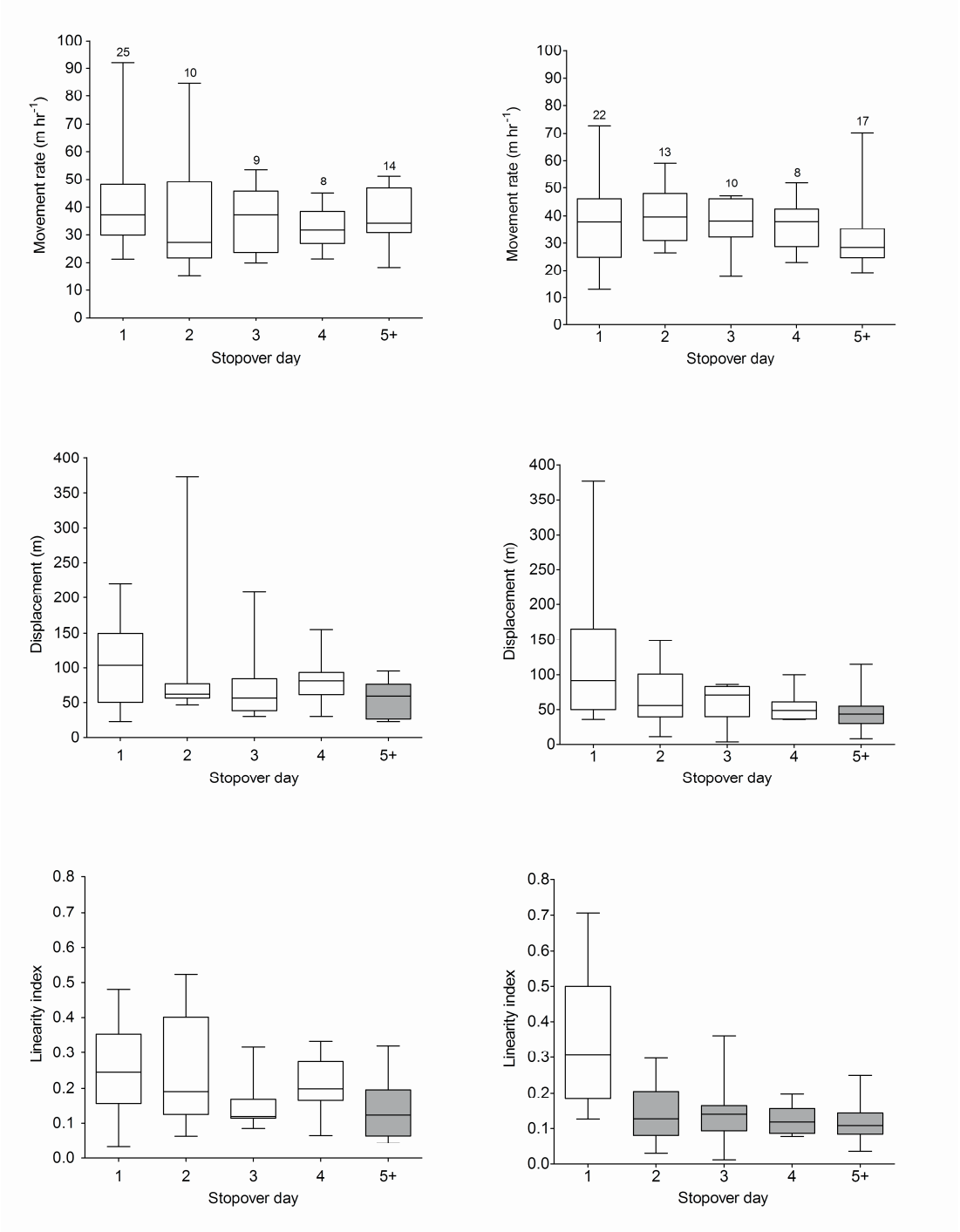

Figure 6.2. Daily changes in three movement parameters of ovenbirds during spring (left) and autumn (right) 2009 stopovers in Prospect Park, Brooklyn, New York. Box plot whiskers show value ranges and boxes show median values and the 25th and 75th percentiles. Sample sizes are shown above bars. Individual days that differed significantly from the first day are indicated by shading; days represented by the same type of box (i.e., open, shaded) did not differ from each other (Tukey's HSD post-hoc tests).

Autumn

Twenty-four ovenbirds were radio-tagged during autumn and transmitters fell off two birds before their departure. The first ovenbird was tagged 10 September and the final tagged ovenbird left the site 4 October. Birds stopped over for an average of 2.9 ± 0.7 d (n = 22). Eleven (50%) birds departed the first night after their capture and the longest stopover lasted 14 d. Durations of spring and autumn stopovers did not differ (Table 6.1).

Autumn migrants also remained close to their capture/release location. The farthest that birds moved from their release point at any time during the stopover averaged 238 ± 35 m (range = 54-778 m). As in spring, birds were not found in non-forested areas but some individuals crossed park roads or open fields to reach other wooded sections of the park.

Overall, ovenbird movement behaviour significantly differed from day to day (Wilk's $\lambda = 0.28$, $F_{12, 166} = 8.47$, $P < 0.001$; Fig. 6.2). In independent analyses, differences in movement rate among days were not significant ($F_{4, 65} = 0.93$, $P = 0.45$), whereas there were significant daily differences in displacement distance ($F_{4, 65} = 4.8$, $P = 0.002$) and linearity ($F_{4,65} = 10.5$, $P < 0.001$). Displacement distances beyond the fourth stopover day were significantly lower than on previous days (Fig. 6.2). Linearity declined more rapidly than during spring stopovers, with index values from day two onwards being significantly lower than on the first day (Fig. 6.2). Ovenbirds moved more broadly and in a straighter direction on day one than on any other day. Movement parameters on the first stopover day did not differ between birds that departed that night and those that remained additional days (Wilk's $\lambda = 0.87$, $F_{3, 18} = 0.94$, $P = 0.44$). Most birds moved widely

throughout the site on their arrival day and then either resumed migration or settled into a more defined area for the remainder of their stopover.

Thirteen birds were tracked long enough to quantify area usage. Individual variation was high, with estimates ranging 0.7-15.8 ha (at 95%). Seven birds (54%) showed significant site fidelity and moved non-randomly (all $P < 0.04$). Home ranges during autumn averaged 23% smaller than during spring, but the size difference was non-significant (Table 6.1).

More ovenbirds (10 of 24) were considered lean and there was more individual variation in fat mass during autumn, but overall, average autumn fat mass (13.3 ± 1.2 % of total body mass) was not significantly different from spring (Table 6.1). In contrast to spring, some first-day movement behaviours during autumn were associated with fat stores. Fat negatively influenced first-day movement rate ($r^2 = 0.25$, $F_{1, 20} = 6.5$, $P = 0.019$) and displacement distance ($r^2 = 0.24$, $F_{1, 20} = 6.2$, $P = 0.022$); fatter birds moved more slowly and remained closer to their capture location than leaner birds. As in spring, fat content during autumn was unrelated to first-day linearity index ($r^2 = 0.06$, $F_{1, 20} = 1.24$, $P = 0.28$), total home range size ($r^2 = 0.11$, $F_{1,11} = 1.28$, $P = 0.28$), and MSD ($r_S = -0.06$, $P = 0.79$).

DISCUSSION

Movement patterns

Radio-tracking ovenbirds in the United States' largest city provided some of the first detailed information on how landbird migrants utilize stopover habitats within heavily urbanized landscapes (see also Matthews and Rodewald 2010a, b). My study site was a

highly isolated habitat fragment located in one of the most densely populated, urban areas of North America. Yet, the spatial behaviour of ovenbirds in Prospect Park was in many ways similar to what has been consistently observed in passerine migrants at non-urban stopover sites. Specifically, bird movements upon arrival were characteristic of exploration and searching, and then became more localized within defined areas later in the stopover period. Ovenbirds showed this same pattern during spring stopovers in non-urban forests of coastal Mississippi, USA (Buler 2006). There, ovenbirds exhibited exploratory, linear movements on the first day of a stopover, followed by relatively area-restricted movements the next day. Migrant summer tanagers (*Piranga rubra*) on a barrier island off the Mississippi coast behaved similarly (Aborn and Moore 1997). Paxton et al. (2008) documented increasingly aggregated movements of Wilson's warblers (*Wilsonia pusilla*) during the course of spring stopovers in southwestern Arizona, USA, and Chernetsov (2005) and Chernetsov and Mukhin (2006) found this trend among European robins (*Erithacus rubecula*) on the Baltic Coast of Russia. I am aware of only one previous investigation of migrant songbird spatial behaviour in an urban area (Matthews and Rodewald 2010a). Matthews and Rodewald (2010a) measured movement rates of radio-tagged Swainson's thrushes (*Catharus ustulatus*) in Columbus, Ohio, USA during spring migration but did not examine daily displacement or linearity. Movement rates on the first two days of stopover did not differ from each other, but it cannot be determined from this information alone whether or not birds ever settled into defined areas.

Differences in GPS format resolution prevented legitimate statistical comparisons of movement parameters between seasons, but generally, ovenbird settling in Prospect

Park occurred more slowly during spring than autumn. During spring, movement linearity did not significantly decrease until the fifth stopover day, whereas during autumn, exploratory behaviour appeared to cease by the second day. Chernetsov (2005) and Chernetsov and Mukhin (2006) found an opposite pattern, where European robins settled slightly faster during spring than autumn. Why search and settling times would differ between seasons is unclear. In my study, it is possible the energetic needs of spring and autumn migrants differed, with the greater temporal constraints and faster pace of spring migration (Berthold 2001, Stutchbury et al. 2008) requiring spring ovenbirds to forage more widely throughout the site to meet energy demands. Plasma triglyceride levels of ovenbirds sampled in Prospect Park 2007-2008 indicated more rapid refueling during spring than autumn stopovers (unpublished data) but it is unknown whether this exclusively reflects seasonal differences in foraging effort. Another explanation is that the greater density of migrants in the park during spring than autumn (based on capture rates) increased competition and it took ovenbirds longer to find unoccupied areas. Stopover territory defense by landbird species, including ovenbirds, has been observed (Rappole and Warner 1976, Bibby and Green 1980, Dierschke et al. 2005, Buler 2006, but see Chernetsov and Mukhin 2006) and it is possible newly arrived individuals were being displaced by established birds. Lastly, the more distinct patterns found in autumn may have simply resulted from the higher resolution GPS coordinate format used to record bird locations. The resolution in spring may have been too coarse to detect true differences in fine-scale movements between the first few stopover days.

Stopover duration

There was a wide range of MSD during both seasons, with many birds departing within one day and some others remaining for nearly a week. High intraspecific variation in stopover duration at a given site is common among passerine migrants (e.g., Morris et al. 1996, Tsvey et al. 2007, Hays 2008). The stopover durations of ovenbirds in Prospect Park were comparable to those of ovenbirds elsewhere in New York City (Chapter V) and Swainson's thrushes in urban forests of Ohio, USA (Matthews and Rodewald 2010b). Stopover durations were also similar to those of spring migrant ovenbirds in non-urban habitats along the Gulf of Mexico (Moore and Kerlinger 1987, Buler 2006) and the coast of Maine (Morris et al. 1996).

Stopover periods of ovenbirds in Prospect Park did not differ between seasons. Autumn stopovers are usually longer than spring stopovers in passerine migrants (e.g., Rguibi-Idrissi et al. 2003, Stutchbury et al. 2008) for several suspected reasons (Berthold 2001, Bauchinger and Klaassen 2005), but the pattern is only general and not always found (Morris and Glasgow 2001, Chernetsov and Muhkin 2006).

Home range

Individual variation in home range size was high during both seasons. Average area usage by ovenbirds in Prospect Park during both seasons was generally greater than what has been reported for passerine migrants elsewhere; although, inconsistent sampling and home range estimation methodologies, which can produce dramatically different results, hinder comparisons between telemetry studies (Kernohan et al. 2001, Borger et al. 2006). Buler (2006) measured area usage of spring migrant ovenbirds in Mississippi on their

first stopover day and subsequent days separately; 95% fixed kernel home range size averaged 1.5 ha during the first day and 0.6 ha on following days. European robins on the Baltic Coast had mean 95% fixed kernel home ranges of 0.4 ha during spring and autumn (Chernetsov and Mukhin 2006). Minimum convex polygon home ranges of Swainson's thrushes during autumn stopovers in northern California averaged 1.9 ha (Tietz and Johnson 2007). Mean 50% fixed kernel home ranges of Swainson's thrushes in various urban forest fragments of Columbus, Ohio ranged approximately 0.4 – 3.0 ha during spring (calculated from Fig. 4 in Matthews and Rodewald 2010a) and in some cases appeared constrained by patch size. In this study, even the largest 95% fixed kernel home ranges of ovenbirds during spring and autumn represented only 16% and 13% of the 100 ha forest area, respectively, suggesting forest size in Prospect Park exceeds the area requirements of individual migrant ovenbirds.

Influence of arrival condition

Stopover behaviour is expected to be largely condition-dependent. A scenario in which lean birds must forage widely and intensively at the expense of increased predation risk while fatter birds with little need to refuel can remain sedentary and less exposed to predators as they await departure (Chernetsov 2006) has intuitive appeal. Indeed, lean ovenbirds and other passerine migrants moved faster, more frequently, and/or covered greater distances than fatter conspecifics during spring stopovers along the Gulf of Mexico (Loria and Moore 1990, Aborn and Moore 1997, Buler 2006). Similarly, lean Swainson's thrushes during spring stopovers in Ohio, USA had higher movement rates than fatter thrushes (Matthews and Rodewald 2010a). However, an alternative and

converse scenario is also plausible. In this scenario, lean birds cannot afford temporal and energetic costs of prolonged exploration and choose to acquire resources from a small area encountered early, while fatter birds invest time and energy in extended searching for the most optimal habitat (Chernetsov 2006). First-day movement patterns of ovenbirds in Prospect Park were not influenced by their condition (i.e., fat mass) during spring, but during fall, fatter birds moved at a slower rate and were closer to their capture location at the end of the day than leaner birds. Chernetsov and Mukhin (2006) found European robin spatial behaviour was not associated with fat stores during spring or autumn stopovers on the Baltic Coast. Wilson's warblers also showed no relationship between their arrival condition and movement patterns during spring stopovers in Arizona, USA (Paxton et al. 2008). Inconsistencies between studies may be due to the possible occurrence of both scenarios (Chernetsov 2006) or differing influences on bird movements from other factors (e.g., predation risk, weather, resource distribution).

Many studies have shown passerine migrant stopover durations to be mediated by energetic condition upon arrival; lean birds tend to remain at stopover sites longer than fat birds (Cherry 1982, Loria and Moore 1990, Yong and Moore 1997, Matthews and Rodewald 2010b; but see Salewski and Schaub 2007). Ovenbirds previously studied in a different New York City park clearly fit this trend (Chapter V). Arrival condition of ovenbirds in Prospect Park, however, did not significantly influence their departure decisions during either season. On the Gulf of Mexico, it was weather and prey availability, and not energetic condition that most significantly affected ovenbird stopover duration (Buler 2006). Refueling rate, distance from final destination, time of season, and predation risk can also influence the length of time passerine migrants spend

at a stopover site (Yong and Moore 1997, Åkesson and Hedenström 2000, Danhardt and Lindström 2001, Dierschke and Delingat 2001, Hays 2008, Schaub et al. 2008). Other such factors likely contributed to ovenbird departures from Prospect Park more so than arrival condition.

CONCLUSION

Decreasing daily exploration by ovenbirds in Prospect Park suggests they eventually encountered and occupied suitable stopover habitat. More broadly, the similarity of their spatial behaviour to that of passerine migrants studied at other stopover sites implies they are utilizing this urban stopover habitat in a similar fashion as less-disturbed, larger forest tracts elsewhere. My findings do not support the speculation that urban stopover habitats likely offer poor conditions for landbird migrants and are only used abruptly in times of urgency when alternatives are unavailable (Mehlman et al. 2005). Indeed, at least half of the birds I studied stopped over for multiple days during spring and autumn, and bird movements during both seasons were indicative of an ability to search for, locate, and occupy adequate habitat patches. These results are consistent with earlier suggestions that habitats remaining within human-dominated landscapes can in fact represent suitable stopover sites for migrating landbirds (Seewagen and Slayton 2008, Matthews 2008, Craves 2009).

It is now widely recognized that meeting the habitat requirements of migration is integral to successful migratory landbird conservation strategies which at one time focused only on issues concerning breeding and over-wintering areas (McCann et al. 1993, Mehlman et al. 2005). However, identifying important stopover sites and setting

conservation priorities have been slowed by an incomplete understanding of migrant stopover habitat selection processes and migrant ecology and behaviour at stopover sites (Petit 2000, Mehlman et al. 2005, Carlisle et al. 2009). Much progress has been made in recent years towards filling these knowledge gaps, but even the most basic information on migrant use of urban stopover habitats is still lacking. Further study is needed to allow land managers in metropolitan areas who strive to provide quality stopover habitats for landbird migrants to make more science-based decisions.

LITERATURE CITED

Aborn DA, Moore FR (1997) Patterns of movement by summer tanagers (*Piranga rubra)* during migratory stopover: a telemetry study. Behaviour 134: 1-24.

Åkesson S, Hedenström A (2000) Wind selectivity of migratory flight departures in birds. Behavioral Ecology and Sociobiology 47: 140-144.

Alerstam T, Hedenström A (1998) The development of bird migration theory. Journal of Avian Biology 29: 343-369.

Bauchinger U, Klaassen M (2005) Longer days in spring than in autumn accelerate migration speed of passerine birds. Journal of Avian Biology 36: 3-5.

Bayne EM, Hobson KA (2001) Movement patterns of adult male ovenbirds during the post-fledging period in fragmented and forested boreal landscapes. Condor 103: 343-351.

Berthold P (2001) Bird migration: a general survey. Oxford University Press, New York.

Beyer HL (2004) Hawth's Analysis Tools for ArcGIS. http://www.spatialecology.com /htools. Accessed June 2009.

Bibby CJ, Green RE (1980) Foraging behaviour of migrant pied flycatchers, *Ficedula hypoleuca*, on temporary territories. Journal of Animal Ecology 49: 507-521

Borger L, Franconi N, De Michele G, Gantz A, Meschi F, Manica A, Lovari S, Coulson T (2006) Effects of sampling regime on the mean and variance of home range size estimates. Journal of Animal Ecology 75: 1393-1405.

Bowlin MS, Cochran WW, Wikelski MC (2005) Biotelemetry of New World thrushes during migration: physiology, energetics and orientation in the wild. Integrative and Comparative Biology 45: 295-304

Brawn JD, Stotz DF (2001) The importance of the Chicago region and the "Chicago Wilderness" initiative for avian conservation. Pp 509-522 in: Avian ecology and conservation in an urbanizing world (Marzluff JM, Bowman R, Donnelly R, eds). Kluwer Press, Boston.

Brigham R (1989) Effects of radio transmitters on the foraging behavior of barn swallows. Wilson Bulletin 101: 505-506.

Brown DR (2006) Food supply and the dry season ecology of a tropical resident bird community and an over-wintering migrant bird species. Dissertation, Tulane University, New Orleans, LA.

Buler JJ (2006) Understanding habitat use by landbirds during migration along the Mississippi Gulf Coast using a scale-dependent approach. Dissertation, University of Southern Mississippi, Hattiesburg, MS.

Buler JJ, Moore FR, Woltmann S (2007) A multi-scale examination of stopover habitat use by birds. Ecology 88: 1789-1802.

Carlisle JD, Skaken SK, Kus BE, Van Riper III C, Paxton KL, Kelly JF (2009) Landbird migration in the American West: Recent progress and future research directions. Condor 111: 211-225.

Cerasale DJ, Guglielmo CG (2010) An integrative assessment of the effects of tamarisk on stopover ecology of a long-distance migrant along the San Pedro River, Arizona. Auk 127: 636-646.

Chapman F (1910) Birds of the vicinity of New York City. American Museum Journal 6: 81-102.

Chernetsov N (2005) Spatial behavior of medium and long-distance migrants at

stopovers studied by radio tracking. Annals of the New York Academy of Sciences 1046: 242-252.

Chernetsov N (2006) Habitat selection by nocturnal passerine migrants en route: mechanisms and results. Journal of Ornithology 147: 185-191.

Chernetsov N, Mukhin A (2006) Spatial behavior of European Robins during migratory stopovers: a telemetry study. Wilson Bulletin 118: 364-373.

Cherry JD (1982) Fat deposition and length of stopover of migrant white-crowned sparrows. Auk 99: 725-732.

Craves JA (2009) A fifteen year study of fall stopover patterns of *Catharus* thrushes at an inland, urban site. Wilson Journal of Ornithology 121:112-118.

Danhardt J, Lindström A (2001) Optimal departure decisions of songbirds from an experimental stopover site and the significance of weather. Animal Behavior 62: 235-243.

DeCandido R, Muir AA, Gargiullo MB (2004) A first approximation of the historical and extant vascular flora of New York City: Implications for native plant species conservation. Journal of the Torrey Botanical Society 131: 243-251.

DeCandido R, Allen D (2005) First confirmed nesting of the Pine Warbler (*Dendroica pinus*) in New York City. Kingbird 55: 328-334.

Dierschke V, Delingat J (2001) Stopover behaviour and departure decision of Northern Wheatears, *Oenanthe oenanthe*, facing different onward non-stop flight distances. Behavioral Ecology and Sociobiology 50: 535-545.

Dierschke V, Mendel B, Schmaljohann H (2005) Differential timing of spring migration

in northern wheatears Oenanthe oenanthe: hurried males or weak females? Behavioral Ecology and Sociobiology 57: 470-480.

Fowle M, Kerlinger P (2001) The New York City Audubon Society guide to finding birds in the metropolitan area. Cornell University press, New York.

Gaunt AS, Oring LW, Able KP, Anderson DW, Baptista LF, Barlow JC, Wingfield JC (1997) Guidelines to the use of wild birds in research. Ornithological Council, Washington D.C.

Griscom L (1923) Birds of the New York City region. American Museum of Natural History Handbook Series 9.

Hays QR (2008) Stopover behavior and refueling physiology in relation to migration distance in Wilson's Warblers (*Wilsonia pusilla*). Thesis. University of Western Ontario, London, ON.

Hooge PN, Eichenlaub B (2000) Animal movement extension to Arcview. Ver 2.0. Alaska Science Center, Anchorage.

Karasov WH, Pinshow B (2000) Test for physiological limitation to nutrient assimilation in a long-distance passerine migrant at a springtime stopover site. Physiological and Biochemical Zoology 73: 335-343.

Kernohan BJ, Gitzen RA, Millspaugh JJ (2001) Analysis of animal space use and movements. Pp 125-166 in: Radio tracking and animal populations (Millspaugh J, Marzluff J, eds). Academic Press, San Diego.

Ktitorov P, Barlein F, Dubinin M (2008) The importance of landscape context for songbirds on migration: body mass gain is related to habitat cover. Landscape Ecology 23: 169-179.

Kokko H (1999) Competition for early arrival in migratory birds. Journal of Animal Ecology 68: 940-950.

Lindstrom A, Alerstam T (1992) Optimal fat loads in migrating birds: A test of the time minimization hypothesis. American Naturalist 140: 477-491.

Loria DE, Moore FR (1990) Energy demands of migration on Red-eyed Vireos, *Vireo olivaceus*. Behavioral Ecology 1: 24-35.

Matthews SN (2008) Stopover habitat utilization by migratory landbirds within urbanizing landscapes of central Ohio. Dissertation. Ohio State University, Columbus, OH.

Matthews S, Rodewald P (2010a). Movement behaviour of a forest songbird in an urbanized landscape: the relative importance of patch-level effects and body condition during migratory stopover. Landscape Ecology 25: 955-965.

Matthews S, Rodewald P (2010b). Urban forest patches and stopover duration of migratory Swainson's thrushes. Condor 112: 96-104.

McCann JM, Mabey SE, Niles LJ, Bartlett C, Kerlinger P (1993) A regional study of coastal migratory stopover habitat for Neotropical migrant songbirds: Land management implications. Transactions of the North American Wildlife and Natural Resources Conference 58: 398-407.

Mehlman DW, Mabey SE, Ewert DN, Duncan C, Abel B, Cimprich D, Sutter RD, Woodrey MS (2005) Conserving stopover sites for forest-dwelling migratory landbirds. Auk 122:1281-1290.

Mittelbach M, Crewdson M (1998) Wild New York: A guide to the wildlife, wild places, and natural phenomena of New York City. Random House, New York.

Moore FR, Kerlinger P (1987) Stopover and fat deposition by North American wood warblers (Parulinae) following spring migration over the Gulf of Mexico. Oecologia 74: 47-54.

Morris SR, Holmes DW, Richmond ME (1996) A ten year study of the stopover patterns of migratory passerines during fall migration on Appledore Island, Maine. Condor 98: 395-409.

Morris SR, Glasgow JL (2001) Comparison of spring and fall migration of American Redstarts on Appledore Island, Maine. Wilson Bulletin 113: 202-210.

Naef-Daenzer B (1994) Radiotracking of Great and Blue tits: new tools to assess territoriality, home-range use and resource distribution. Ardea 82: 335-347.

Paxton KL, Van Riper III C, O'Brien C (2008) Movement patterns and stopover ecology of Wilson's warblers during spring migration on the lower Colorado River in southwestern Arizona. Condor 110: 672-681.

Pennington DN, Hansel J, Blair RB (2008) The conservation value of urban riparian areas for landbirds during spring migration: Land cover, scale, and vegetation effects. Biological Conservation 141: 1235-1248.

Petit DR (2000) Habitat use by landbirds along Neartic-Neotropical migration routes: Implications for conservation of stopover habitats. Studies in Avian Biology 20: 15-33.

Rae LF, Mitchell GW, Mauck RA, Guglielmo CG, Norris DR (2009) Radio transmitters do not affect the body condition of Savannah Sparrows during the fall premigratory period. Journal of Field Ornithology 80: 419-426.

Raim A (1978) A radio transmitter attachment for small passerine birds. Bird-Banding 49: 326-332.

Rappole JH, Warner DW (1976) Relationships between behavior, physiology and weather in avian transients at a migration stopover site. Oecologia 26: 193-212.

Rappole JH, Derrickson SR, Hubàlek (2000) Migratory birds and spread of West Nile Virus in the western hemisphere. Emerging Infectious Diseases 6: 319-328.

Rguibi-Idrissi H, Julliard R, Bairlein F (2003) Variation in the stopover duration of reed warblers Acrocephalus scirpaceus in Morocco: effects of season, age and site. Ibis 145: 650-656.

Rodewald PG, Brittingham MC (2004) Stopover habitats of landbirds during fall: use of edge-dominated and early-successional forests. Auk 121: 1040-1055.

Rodewald PG, Brittingham MC (2007) Stopover habitat use by spring migrant landbirds: The roles of habitat structure, leaf development and food availability. Auk 124: 1063-1074.

Salewski V, Schaub M (2007) Stopover duration of Palearctic passerine migrants in the western Sahara – independent of fat stores? Ibis 149: 223-236.

Sandberg R, Moore FR (1996) Fat stores and arrival on the breeding grounds: reproductive consequences for passerine migrants. Oikos 77: 577-581.

Schaub M, Jenni L, Bairlein F (2008) Fuel stores, fuel accumulation, and the decision to depart from a migration stopover site. Behavioral Ecology 19: 657-666.

Seaman DE, Millspaugh JJ, Kernohan BJ, Brundige GC, Raedeke KJ, Gitzen RA (1999) Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63: 739-747.

Seewagen CL (2008) Lipid content of Nearctic-neotropical migratory passerines killed during stopovers in a New York City park. Northeastern Naturalist 15: 87-96

Seewagen CL, Slayton EJ (2008) Mass changes of migratory landbirds during stopovers in a New York City park. Wilson Journal of Ornithology 120: 296-303.

Seewagen CL, Slayton EJ, Guglielmo CG (2010) Passerine migrant stopover duration and spatial behaviour at an urban stopover site. Acta Oecologica. doi10.1016/ j.actao.2010.06.005.

Simons TR, Peason SM, Moore FR (2000) Application of spatial models to the stopover ecology of trans-Gulf migrants. Studies in Avian Biology 20: 4-14.

Smith RJ, Moore FR (2003) Arrival fat and reproductive performance in a long-distance passerine migrant. Oecologia 134: 325-331.

Strode PK (2009) Spring tree species use by migrating yellow-rumped warblers in relation to phenology and food availability. Wilson Journal of Ornithology 121: 457-468.

Stutchbury BJM, Tarof SA, Done T, Gow E, Kramer PM, Tautin J, Fox JW, Afanasyev V (2008) Tracking long-distance songbird migration by using geolocators. Science 323: 896.

Sykes Jr PW, Carpenter J, Holzman S, Geissler P (1990) Evaluation of three miniature radio transmitter attachment methods for small passerines. Wildlife Society Bulletin 18: 41-48.

Tietz JR, Johnson MD (2007) Stopover ecology and habitat selection of juvenile Swainson's thrushes during fall migration along the northern California coast. Condor 109: 795-807.

Tsvey A, Bulyuk VN, Kosarev V (2007) Influence of body condition and weather on departures of first-year European Robins, *Erithacus rubecula*, from an autumn migratory stopover site. Behavioral Ecology and Sociobiology 61: 1665-1674.

U.S. Census Bureau (2010) State and County Quick Facts. http://quickfacts.census.gov /qfd/states/36000.html. Accessed February 2010.

Van Horn MA, Donovan TM (1994) Ovenbird (*Seiurus aurocapillus*). No. 182 in: The birds of North America (Poole A, Gill F, eds.). The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington D.C.

Wells JV (1998) Important bird areas of New York State. National Audubon Society, Albany.

White GC, Garrott RA (1990) Analysis of wildlife radio-tracking data. Academic Press, San Diego.

Wikelski M, Tarlow EM, Raim A, Diehl RH, Larkin RP, Visser GH (2003) Costs of migration in free-flying songbirds. Nature 423: 704.

Yong W, Moore FR (1997) Spring stopover of intercontinental migratory thrushes along the northern coast of the Gulf of Mexico. Auk 114: 263-278.

Table 6.1. Fat mass, minimum stopover duration (MSD), and fixed kernel home range size (measured at three isopleth levels) of ovenbirds radio-tracked during spring and autumn 2009 stopovers in Prospect Park, Brooklyn, New York do not differ between seasons. Seasonal differences in fat mass and MSD tested with a Welch-corrected *t*-test and Mann-Whitney *U*-test, respectively. Spring and autumn 95% home range sizes compared with a Student's *t*-test. Values are means ± SE.

	Spring	Autumn	df	*P*
Fat (g)	3.1 ± 0.1	3.0 ± 0.4	27	0.70
n	33	22		
MSD (d)	2.8 ± 0.5	2.9 ± 0.7	1	0.92
n	27	22		
95% home range (ha)	4.8 ± 1.1	3.7 ± 1.2	26	0.48
n	15	13		
90% home range (ha)	3.6 ± 0.8	2.8 ± 0.9		
50% home range (ha)	0.9 ± 0.2	0.7 ± 0.2		

CHAPTER VII

CHAPTER SUMMARIES AND CONCLUDING REMARKS

The above studies have shed new light on the stopover biology of migrants in urban ecosystems. Collectively they have provided a comprehensive assessment of the quality of these unique habitats as migratory bird stopover sites. Refueling rates, biphasic mass gains, stopover durations, area usage, and search and settling behaviours of migrants in New York City indicated the urban habitats examined are functioning in the same fashion as larger, less-disturbed, stopover sites elsewhere. I found no evidence to suggest that stopover refueling conditions within one of the world's most urbanized landscapes were inadequate for migrating landbirds.

RESEARCH SUMMARY

In Chapter II, I showed that condition indices commonly used in field-studies of birds can provide accurate measures of fat content. I developed models that can be used to simply and noninvasively quantify the fat mass of avian migrants based on their total body mass and amount of visible subcutaneous fat. These models allowed me in subsequent chapters to show that migrants gained lean body mass in addition to fat mass during stopover refueling, and most spatial behaviours of migrants were uninfluenced by the size of their arrival fat stores. Other, more sophisticated techniques of measuring body composition, such as the QMR method used in Chapters IV and V, are often cost-prohibitive or otherwise unavailable to many researchers. Condition indices and predictive models

provide estimates of fat mass with simplicity and accuracy that justifies their continued use in field studies of birds.

Chapter III presented the first application of plasma metabolite profiling and measures of food abundance to assess the quality of stopover sites for passerine migrants in an urban landscape. Many city parks are famous for receiving exceptional concentrations of migrants (Fowle and Kerlinger 2001, Milne 2007), but the resources provided by these habitats, and their ultimate value as stopover sites, has been uncertain (Mehlman et al. 2005). I showed that refueling conditions for migrants in NYC were no poorer than those in the less disturbed habitats examined outside of the city. Plasma metabolite values of multiple species indicated comparable refueling performance between NYC and Westchester County, and measures of arthropod biomass suggested similar food abundance for ground-foraging insectivores in the two areas during both seasons. Migrant refueling rates, as indicated by triglyceride concentrations, in NYC were in some cases higher than those reported in the literature for conspecifics at various non-urban stopover sites. The body mass-time of day regression approach also suggested mass gain occurred in NYC at rates comparable to, or higher than, non-urban habitats elsewhere. These findings are consistent with those of Seewagen and Slayton (2008) and Craves (2009), which provided earlier indications that migrants can successfully increase their body mass during stopovers in urban habitats.

In Chapter IV, QMR body composition analyses and a predictive model developed in Chapter II revealed that part of the total body mass gained by migrants in NYC consisted of lean mass. Lean mass contributed to at least 30% of the individual variation in total body mass or the total body mass gained during stopover refueling.

These findings extend what has been well-established in shorebirds and Old World passerines at geographical barriers to New World passerines and passerines migrating in shorter bouts over more continuously available stopover habitat. Thus protein usage during bird migration appears to be common across broad taxonomic groups, migration systems, and flight distances.

The lean body mass changes observed among migrants in NYC highlight the importance of dietary protein sources, and carry implications for stopover habitat restoration and management practices. To meet their nutrient needs, migrants using these sites will require high-protein foods in addition to the lipid- and carbohydrate-rich foods that maximize fattening rates (Barlein 1998, Karasov and Pinshow 1998). Surveys in Chapter III showed that macroinvertebrate biomass was similar between the urban and non-urban stopover habitats, indicating sufficient protein sources are available to passerine birds in NYC.

In Chapter V, I utilized a small dataset acquired during a pilot study in Bronx Park to examine the influence of arrival fat and lean body mass on stopover duration. The time birds stayed at the stopover site was strongly and negatively related to their arrival fat mass. This result is unsurprising and consistent with several other studies that have shown arrival condition to be a primary determinant of stopover duration (e.g., Cherry 1982, Yong and Moore 1997, Mathews and Rodewald 2010a, Goymann et al. 2010). It is intuitive that birds arriving with small fat stores would remain at a stopover site to refuel for longer periods than birds with larger arrival fat stores. By extension, lean body mass upon arrival should also influence stopover duration when refueling includes the deposition of lean tissues (as shown in Chapter III). Yet I found no relationship between

lean body mass and stopover duration among the migrants radio-tracked in Bronx Park. It is possible a type II error occurred due to the small sample size of only eleven birds. However, Fusani et al. (2009) found that a measure of lean body mass did not affect the migratory restlessness of captive birds, which also indicates lean mass does not influence departure decisions. Further study is needed to clarify how changes in lean body mass affect migrant stopover duration and overall migration time.

In Chapter VI, ovenbirds radio-tracked during spring and autumn stopovers in Prospect Park revealed that migrant behaviour at an urban stopover site was similar in many ways to that of migrants in larger, less disturbed habitats elsewhere. During both seasons birds exhibited a tendency to explore the stopover habitat widely upon arrival and then either resume migration that night or settle in to more defined areas on subsequent days. Migrant movements were indicative of an ability to search for, locate, and occupy suitable microhabitat, and temporary home ranges suggested forest size in Prospect Park is more than sufficient to meet the area requirements of migrating ovenbirds. Matthews and Rodewald (2010b) similarly found that most forest fragments in the Columbus, Ohio metropolitan area were of adequate size for migrating Swainson's thrushes. Most spatiotemporal behaviors of ovenbirds were not condition-mediated in Prospect Park and it is likely other factors such as weather were more influential than arrival condition.

The similarity of the stopover biology of migrants in NYC to that of migrants at other stopover sites implies that migrants are using urban habitats in the same fashion as larger forest tracts elsewhere. My findings do not support previous speculation that migrants only use urban habitats as stopover sites briefly and possibly to moderately

refuel when more suitable alternatives are unavailable (Mehlman et al. 2005). Indeed, migrants (1) often remained in NYC for multiple days, (2) refueled at comparable, and in many cases higher, rates as birds in non-urban areas, (3) increased lean body mass, and (4) exhibited spatiotemporal behaviours that were characteristic of the searching and settling patterns of passerine migrants observed in non-urban sites. These results are in line with the few previous studies of urban stopover biology (Seewagen and Slayton 2008, Craves 2009, Matthews and Rodewald 2010a, b) and add to a small but growing body of evidence that urban habitats can represent suitable stopover sites for migratory landbirds.

There are several potential explanations for why migrants can have successful stopovers in highly disturbed, urban habitats such as those of NYC, and they need not be mutually exclusive. First, although urban forest fragments are typically isolated and surrounded by heavy development, it is possible they retain enough of the natural properties of larger, intact forests to provide the resources passerine migrants need most from stopover habitats. Second, it is possible the behavioural plasticity of birds during migration simply enables them to exploit even the most unfamiliar, atypical habitats (Parrish 2000) and cope with the disturbances and other unique conditions experienced at urban stopover sites. Third, it is possible that urban heat island effects have altered ecosystem processes in ways that are beneficial to migrants and that compensate for the types of degradation commonly associated with urban habitats (e.g., increased edge, soil compaction and erosion, pollution, invasive species). Warmer air temperatures in cities can potentially increase the abundance of terrestrial invertebrates, advance their spring phenology, and prolong their autumn survival (Raupp et al. 2010, Johnson 2007), and in

turn, enhance food sources for insectivorous migrants. Heat island effects also often lead to early spring leaf-out and delayed autumn dormancy of vegetation relative to cooler areas outside of the city (Roetzer et al. 2000, White et al. 2002, Zhang et al. 2004), which may be what initially attracts large numbers of migrating birds to urban habitats (Matthews 2008). Urban habitats could present an interesting model to study the influence that phenological shifts associated with global climate change will have on migratory bird stopover biology.

Regardless of what allows migrants to have successful stopovers in NYC, sufficient stopover conditions appear to be available and costly habitat restoration efforts on behalf of migrating songbirds are not necessarily needed. Resources intended to benefit migrating birds in NYC should be directed at maintaining the stopover sites studied, and others like them, in their present state.

CONCLUDING REMARKS

Breeding birds have been well-studied in cities (Marzluff et al. 2001) and nearly all discussion in the scientific literature about how to manage urban habitats to benefit birds concerns the nesting period exclusively (e.g., Marzluff and Ewing 2001). Migration has been comparatively overlooked. It is telling that in lengthy review articles on the effects of urbanization on birds (Chace and Walsh 2006) and habitat management for birds in urban areas (Marzluff and Ewing 2001), the word “stopover” does not appear once.

Most bird migration studies in cities have examined levels of richness, diversity, and abundance (Brawn and Stotz 2001, Hostettler et al. 2005, Rodewald and Matthews 2005, Pennington et al. 2008). Without discounting the value of the knowledge gained by

such studies, little can be inferred from these metrics about absolute habitat quality (Van Horne 1983, Johnson 2007) because migrant stopover site selection is severely constrained by limited habitat availability in cities. High migrant abundance, diversity, or richness at a given stopover site does not necessarily indicate high quality habitat because migrants may be forced to use poor quality habitats when habitat availability is low. More studies of migrant refueling rates and movement patterns are encouraged to identify high quality and important stopover habitats in urban landscapes.

Stopover biology studies in urban areas can present unique logistical difficulties of which, based on my personal experiences in NYC, I recommend potential researchers be mindful. There are many conveniences of conducting field research in cities compared to more remote settings, but there are many constraints and challenges as well.

Personal safety concerns often restrict the locations and times of day at which research should be conducted, and working alone is usually unwise. Field equipment is also prone to vandalism and theft and cannot be left unattended without risk. Setting up and taking down mist nets at each site each day was not practical in my studies. Nets remained at the sites overnight and were at times vandalized (particularly at the beginning of a new field season). I was informed by park officials that homeless people living in the study sites were likely responsible for the vandalism as retaliation for any intrusion or displacement they incurred from my research activities. Reaching out to people living in the parks by explaining to them the research being conducted and inviting them to observe helped curb incidences of vandalism.

Local political bureaucracy, special interest groups and stakeholders active in public park policy, and competing usages of limited park space can make it difficult to

obtain permission to conduct non-passive bird research in city parks. Outspoken ethical concerns over mist-netting and banding from stakeholders such as local birding communities can add controversy and limit research opportunities, and should be expected. Open communication with local birders and birding organizations, and invitations to become involved in research activities are recommended at the proposal stage as preemptive means to assuage potential resistance and opposition.

Dog walkers are stakeholders whose interests can easily interfere with studies of birds in city parks. Throughout my field seasons, leash laws were poorly obeyed or enforced, and dog walkers often sternly denied my requests to keep their dogs on walking trails and out of wooded areas. Several mist nets were destroyed by dogs running through them, and at times bird capture rates were likely reduced by dogs flushing birds out of the area. Fencing that separates trails and recreational spaces from interior woodlands where mist nets would be placed is a recommended criterion for study site selection. However, fenced areas are usually fenced because they are regenerating or particularly sensitive, and gaining access to such restricted areas can be all the more difficult.

These are only some of the difficulties that researchers may encounter during studies of urban stopover biology and each city likely presents its own set of challenges. Ample time should be allotted to address such matters before studies are targeted to begin. Pilot studies are beneficial and recommended before larger-scale efforts are undertaken.

Prior to the research presented in this dissertation, knowledge of migratory bird stopover biology and stopover habitat quality in urban ecosystems was limited to only a few studies (Matthews 2008, Seewagen and Slayton 2008, Craves 2009). Here, I have

substantially added to our understanding of the ecology and behaviour of migrants in urban areas and provided a more holistic assessment of the quality of urban habitats as migratory bird stopover sites.

My findings are encouraging from a conservation standpoint, as they indicate that small and highly disturbed habitats that may otherwise be of little significance to wildlife have the potential to be valuable stopover sites for migrating birds. However, these results can only be generalized elsewhere with much caution due to the large variation within and among cities in intrinsic and extrinsic habitat characteristics that likely influence site quality. It is hoped that my studies in NYC will encourage investigation of migrant stopover biology and stopover habitat quality in other metropolitan areas of North America and around the world, and ultimately promote more science-based decision-making in cities with regard to migrating birds. It is important to recognize that the conclusions drawn here are not intended to advocate urbanization or other forms of habitat loss without concern for migratory birds. Instead my results should highlight the importance of conserving and effectively managing natural areas even within human-dominated landscapes such as cities. **Ω**

LITERATURE CITED

Barlein F (1998) The effect of diet composition on migratory fuelling in garden warblers *Sylvia borin*. Journal of Avian Biology 29:546-551.

Brawn JD, Stotz DF (2001) The importance of the Chicago region and the "Chicago Wilderness" initiative for avian conservation. Pp. 509-522 in: Avian ecology and conservation in an urbanizing world (Marzluff JM, Bowman R, Donnelly R, eds). Kluwer Press, Boston.

Chace JF, Walsh JJ (2006) Urban effects on native avifauna: a review. Landscape and Urban Planning 74:46-69.

Cherry JD (1982) Fat deposition and length of stopover of migrant white-crowned sparrows. Auk 99:725-732.

Craves JA (2009) A fifteen year study of fall stopover patterns of *Catharus* thrushes at an inland, urban site. Wilson Journal of Ornithology 121:112-118.

Fowle M, Kerlinger P (2001) The New York City Audubon Society guide to finding birds in the metropolitan area. Cornell University Press, New York.

Fusani L, Cardinale M, Carere C, Goymann W (2009) Stopover decision during migration: physiological conditions predict nocturnal restlessness in wild passerines. Biology Letters 5:302-305.

Goymann W, Spina F, Ferri A, Fusani L (2010) Body fat influences departure from stopover sites in migratory birds: evidence from whole-island telemetry. Biology Letters. doi:10.1098/rsbl.2009.1028.

Hostetler M, Duncan S, Paul J (2005) Post-construction effects of an urban development on migrating, resident, and wintering birds. Southeastern Naturalist 4:421-434.

Johnson EA (2007) A seasonal guide to New York City's invertebrates. American Museum of Natural History, New York.

Karasov WH, Pinshow B (1998) Changes in lean mass and in organs of nutrient assimilation in a long-distance passerine migrant at a springtime stopover site. Physiological Zoology 71:435-448.

Marzluff J, Ewing K (2001) Restoration of fragmented landscapes for the conservation of birds: A general framework and specific recommendations for urbanizing landscapes. Restoration Ecology 9:280-292.

Marzluff J, Bowman R, Donnelly R (2001) Avian ecology and conservation in an urbanizing world. Kluwer Academic Publishers, Massachusetts.

Matthews SN (2008) Stopover habitat utilization by migratory landbirds within urbanizing landscapes of central Ohio. Dissertation. Ohio State University, Columbus, OH.

Matthews S, Rodewald P (2010a) Urban forest patches and stopover duration of migratory Swainson's thrushes. Condor 112:96-104.

Matthews S, Rodewald P (2010b) Movement behaviour of a forest songbird in an urbanized landscape: the relative importance of patch-level effects and body condition during migratory stopover. Landscape Ecology 25:955-965.

Mehlman DW, Mabey SE, Ewert DN, Duncan C, Abel B, Cimprich D, Sutter RD, Woodrey MS (2005) Conserving stopover sites for forest-dwelling migratory landbirds. Auk 122:1281-1290.

Milne P (2007) Where to watch birds in world cities. Yale University Press, New Haven.

Parrish JD (2000) Behavioral, energetic, and conservation implications of foraging

plasticity during migration. Studies in Avian Biology 20:53–70.

Pennington DN, Hansel J, Blair RB (2008) The conservation value of urban riparian areas for landbirds during spring migration: Land cover, scale, and vegetation effects. Biological Conservation 141:1235-1248.

Raupp MJ, Shrewsbury PM, Herms DA (2010) Ecology of herbivorous arthropods in urban landscapes. Annual Review of Entomology 55:19-38.

Rodewald PG, SN Matthews (2005) Landbird use of riparian and upland forest stopover habitats in an urban landscape. Condor 107:259-268.

Roetzer T, Wittenzeller M, Haeckel H, Nekovar J (2000) Phenology in central Europe- differences and trends of spring phenophases in urban and rural areas. International Journal of Biometeorology 44:60-66.

Seewagen CL, Slayton EJ (2008) Mass changes of migratory landbirds during stopovers in a New York City park. Wilson Journal of Ornithology 120:296-303.

Van Horne B (1983) Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.

White MA, Nemani RR, Thornton PE, Running SW (2002) Satellite evidence of phenological differences between urbanized and rural areas of the eastern United States deciduous broadleaf forest. Ecosystems 5:260-277.

Yong W, Moore FR (1997) Spring stopover of intercontinental migratory thrushes along the northern coast of the Gulf of Mexico. Auk 114:263-278.

Zhang X, Friedl MA, Schaaf CB, Strahler AH, Schneider A (2004) The footprint of urban climates on vegetation phenology. Geophysical Research Letters 31:L12209. doi: 10.1029/2004GL020137.

APPENDIX 1: ETHICS COMMITTEE APPROVALS

November 5, 2007

Mr. Chad Seewagan
Bird Department
Wildlife Conservation Society

Dear Chad:

I am writing on behalf of the Institutional Animal Care and Use Committee concerning your submission of **PROJECT 07-07: Continuation of 5-12B New York Bird Monitoring Program : the Energetics and Stopover Ecology of Neotropical Migrants in an Urban Park.**

As you are aware, this project has been approved by the IACUC committee. Please forward a summary report with images when complete.

We look forward to hearing from you.

Sincerely,

Robert A. Cook, VMD, MPA
Senior Vice President & General Director
Living Institutions
Wildlife Conservation Society

Dear Chad:

Please be advised that your proposal 08-05 A pilot study of the stopover duration of ovenbirds and Swainson's thrushes in Bronx Park during autumn migration (a component of the Environmental Benefit project settlement with NYS DEC) has been approved by the IACUC committee.

Please plan to go ahead with your study and forward a summary report for the next IACUC meeting which will be announced sometime in January/February.

Joanne Valletta
Office Manager/Executive Assistant
Global Health Programs
Wildlife Conservation Society
2300 Southern Boulevard
Bronx, NY 10460
Phone: 718-220-7100
Fax: 718-220-7126

"When the last individual of a race of living things breathes no more, another heaven and another earth must pass before such a one can be again." William Beebe.

Western

02.25.08
*This is the 2nd Renewal of this protocol
*A Full Protocol submission will be required in 2010

Dear Dr. **Guglielmo**

Your Animal Use Protocol form entitled:

Physiological ecology of migratory birds during stopover refueling

has been approved by the Animal Use Subcommittee.
This approval is valid from **03.01.08 to 02.28.09**
The protocol number for this project remains as **2006-014-02**

1. This number must be indicated when ordering animals for this project.
2. Animals for other projects may not be ordered under this number.
3. If no number appears please contact this office when grant approval is received.
   If the application for funding is not successful and you wish to proceed with the project, request that an internal scientific peer review be performed by the Animal Use Subcommittee office.
4. Purchases of animals other than through this system must be cleared through the ACVS office. Health certificates will be required.

ANIMALS APPROVED FOR 1 YEAR **Highest Pain Level:** C

Species	Other Detail	Housing/Use Locations	Animal # Total for 1 Year
Bird-Wild	Songbird	Field, New York City region	1000
Bird-Wild	Songbird	Bronx Zoo, FLIER	400

REQUIREMENTS/COMMENTS
Please ensure that individual(s) performing procedures on live animals, as described in this protocol, are familiar with the contents of this document.

The University *of* Western Ontario
Animal Use Subcommittee/University Council on Animal Care
Health Sciences Centre, • London, Ontario • CANADA - N6A 5C1
PH: 519-661-2111 ext. 86770 • F: 519-661-2028 • www.uwo.ca/animal

APPENDIX 2: PERMITS

United States Department of the Interior
U.S. GEOLOGICAL SURVEY
PATUXENT WILDLIFE RESEARCH CENTER
BIRD BANDING LABORATORY
12100 BEECH FOREST ROAD STE-4037
LAUREL, MD 20708-4037
301-497-5790

FEDERAL BIRD BANDING PERMIT

Permittee: Personal	Permit Number:	Action:	Action Date:	Issue Date:	Valid Until:
ERIC SLAYTON	23452	Renew	12/02/09	10/12/06	09/30/13
WILDLIFE CONSERVATION SOCIETY 2300 SOUTHERN BLVD BRONX, NY 10460	Signature of Issuing Official, Chief, Bird Banding Laboratory Signature of Permittee				

Permittee agrees to band in accordance with the general conditions of this permit and with the specific authorization/s listed below:

Permittee is Authorized To Band:

All Species Except Waterfowl, Eagles or Endangered/Threatened Species Unless Specified

In the States of:

NY *

With Special Authorization to:

Trap
Use mist nets
Band
Take blood samples

And Additionally Authorized to Use The Following Auxiliary Marking Authorization/s:

Marker Type	Species	Colors	Locations	Comments
01D Tape over alum. Colored Leg Band	COM YELLOWTHROAT GRAY-CHEEK THRUSH NO WATERTHRUSH OVENBIRD SWAINSON'S THRUSH VEERY WOOD THRUSH BLK-AND-WH WARBLER BLK-THR BLUE WARB MAGNOLIA WARBLER AMERICAN REDSTART	Blue, Green, Orange, Red, White, Yellow	New York, NY	
89 Radio Transmitter	OVENBIRD SWAINSON'S THRUSH		Bronx, NY Westchester, NY Kings, NY	NTE 3% total body weight, glue attachment, 164 to 165 MHz
01A Plastic Colored Leg Band	RED-WING BLACKBIRD	Dark Blue, Green, Hot Pink, Light Blue, Light Green, Pink	Orange, NY Bronx, NY	

DEPARTMENT OF THE INTERIOR
U.S. FISH AND WILDLIFE SERVICE

3-201
(1/97)

FEDERAL FISH AND WILDLIFE PERMIT

1. PERMITTEE

WILDLIFE CONSERVATION SOCIETY
2300 SOUTHERN BLVD.
BRONX, NY 10460
U.S.A.

2. AUTHORITY-STATUTES
16 USC 703-712

REGULATIONS *(Attached)*
50 CFR PART 13
50 CFR 21.21

3. NUMBER
MB841861-0

4. RENEWABLE
☒ YES
☐ NO

5. MAY COPY
☒ YES
☐ NO

6. EFFECTIVE
08/01/2008

7. EXPIRES
07/31/2011

8. NAME AND TITLE OF PRINCIPAL OFFICER *(If #1 is a business)*
ROBERT A COOK
SENIOR VP & GENERAL DIRECTOR

9. TYPE OF PERMIT
MIGRATORY BIRD IMPORT/EXPORT

10. LOCATION WHERE AUTHORIZED ACTIVITY MAY BE CONDUCTED
ANY U.S. FISH & WILDLIFE SERVICE DESIGNATED PORT
TEL: 718-220-5100

11. CONDITIONS AND AUTHORIZATIONS:

A. GENERAL CONDITIONS SET OUT IN SUBPART D OF 50 CFR 13, AND SPECIFIC CONDITIONS CONTAINED IN FEDERAL REGULATIONS CITED IN BLOCK #2 ABOVE, ARE HEREBY MADE A PART OF THIS PERMIT. ALL ACTIVITIES AUTHORIZED HEREIN MUST BE CARRIED OUT IN ACCORD WITH AND FOR THE PURPOSES DESCRIBED IN THE APPLICATION SUBMITTED. CONTINUED VALIDITY, OR RENEWAL, OF THIS PERMIT IS SUBJECT TO COMPLETE AND TIMELY COMPLIANCE WITH ALL APPLICABLE CONDITIONS, INCLUDING THE FILING OF ALL REQUIRED INFORMATION AND REPORTS.

B. THE VALIDITY OF THIS PERMIT IS ALSO CONDITIONED UPON STRICT OBSERVANCE OF ALL APPLICABLE FOREIGN, STATE, LOCAL OR OTHER FEDERAL LAW.

C. VALID FOR USE BY PERMITTEE NAMED ABOVE.

D. Authorized to import or export lawfully acquired migratory birds listed in 50 CFR Part 10, including carcasses, blood and/or tissue, parts, nests or egg specimens for scientific, research and/or educational purposes.

E. Permittee must notify Wildlife Inspectors at least 72 hours prior to import or export.

F. Authorized subpermittees: Employees of The Wildlife Conservation Society

G. Permittee must also comply with the attached Migratory Bird Import/Export Permit Standard Conditions.

☒ ADDITIONAL CONDITIONS AND AUTHORIZATIONS ALSO APPLY

12. REPORTING REQUIREMENTS

RD, MIGRATORY BIRDS & STATE PROGRAMS

DATE
07/21/2008

New York State Department of Environmental Conservation
Division of Fish, Wildlife and Marine Resources - Special Licenses Unit
625 Broadway
Albany, NY 12233-4752
Phone Number (518) 402-8985
Fax Number: (518) 402-8925

NEW YORK STATE FISH AND WILDLIFE LICENSE

License Type: Collect or Possess: Banding License Number: 44

Licensee:

ERIC J SLAYTON
WILDLIFE CONSERVATION SOCIETY
2300 SOUTHERN BLVD ORNITHOLOGY DEPT
BRONX, NY 10460

Fee Amount: $10.00
Effective Date: 02/27/2009
Expiration Date: 02/28/2014
Region: 2 County: BRONX
Home Phone Number: (631) 935-3135
Business Phone Number: (631) 935-3135

DOB: 7/3/1965

Statutory Authority:

6NYCRR Part 175 ECL 11-0515

Conditions:

1. A. Please read all license conditions BEFORE conducting any activity pursuant to this license.

   B. The licensee assumes all liability and responsibility for any activities conducted under the authority of this license or any actions resulting from activities authorized by the license.

   C. This license may be revoked for any of the following reasons:
   i. licensee provided materially false or inaccurate statements in his or her application, supporting documentation or on required reports;
   ii. failure by the licensee to comply with any terms or conditions of this license;
   iii. licensee exceeds the scope of the purpose or activities described in his or her application for this license;
   iv. licensee fails to comply with any provisions of the NYS Environmental Conservation Law, any other State or Federal laws or regulations of the Department directly related to the licensed activity;
   v. licensee submits a check, money order or voucher for this license or application for this license that is subsequently returned to the Department for insufficient funds or nonpayment after the license has been issued.

   D. The renewal of this license is the responsibility of the licensee. This license is deemed expired on the date of expiration listed on the license unless otherwise notified by the Department.

   E. Direct all questions concerning this license to the Special Licenses Unit (518) 402-8985.

2. A. The licensee is authorized to collect, temporarily possess, mark with approved federal bands and release migratory birds for banding purposes.

   B. This license is invalid without a corresponding valid Federal Permit for banding.

   C. No endangered/threatened species may be collected or possessed pursuant to this license.

   D. On or before February 1st of each year, the licensee must submit a written statement to the NYS DEC Special Licenses Unit indicating that the licensee has or intends to comply with all reporting requirements of his or her Federal Permit for the previous year. This statement must contain the licensee's current address.

   E. If raptors are banded, the licensee must submit a copy of all reports involving raptors, required by the licensee's Federal Banding Permit, to the NYS DEC Endangered Species Unit, 625 Broadway, Albany, NY 12233-4754. In addition, please fill out the enclosed "New York State Raptor Nest Database" form for any of the following species of Special Concern: all Osprey, Sharp-shinned Hawks, Cooper's Hawks, Northern Goshawks and Red-shouldered Hawks if applicable AND mail to the Endangered Species Unit.

APPENDIX 3: COPYRIGHT RELEASES

JOHN WILEY AND SONS LICENSE TERMS AND CONDITIONS

Aug 26, 2010

This is a License Agreement between Wildlife Conservation Society ("You") and John Wiley and Sons ("John Wiley and Sons") provided by Copyright Clearance Center ("CCC"). The license consists of your order details, the terms and conditions provided by John Wiley and Sons, and the payment terms and conditions.

All payments must be made in full to CCC. For payment instructions, please see information listed at the bottom of this form.

License Number	2496530943758
License date	Aug 26, 2010
Licensed content publisher	John Wiley and Sons
Licensed content publication	Journal of Field Ornithology
Licensed content title	An evaluation of condition indices and predictive models for noninvasive estimates of lipid mass of migrating Common Yellowthroats, Ovenbirds, and Swainson's Thrushes
Licensed content author	Chad L. Seewagen
Licensed content date	Mar 1, 2008
Start page	80
End page	86
Type of use	Dissertation/Thesis
Requestor type	Author of this Wiley article
Format	Print and electronic
Portion	Full article
Will you be translating?	No
Order reference number	
Total	0.00 USD

Terms and Conditions

TERMS AND CONDITIONS

This copyrighted material is owned by or exclusively licensed to John Wiley & Sons, Inc. or one if its group companies (each a "Wiley Company") or a society for whom a Wiley Company has exclusive publishing rights in relation to a particular journal (collectively "WILEY"). By clicking "accept" in connection with completing this licensing transaction, you agree that the following terms and conditions apply to this transaction (along with the billing and payment terms and conditions established by the Copyright Clearance Center Inc., ("CCC's Billing and Payment terms and conditions"), at the time that you opened your Rightslink account (these are available at any time at http://myaccount.copyright.com).

Terms and Conditions

1. The materials you have requested permission to reproduce (the "Materials") are protected by copyright.

From: Clait E. Braun [mailto:sg-wtp@juno.com]
Sent: Monday, August 23, 2010 11:23 AM
To: Seewagen, Chad
Subject: 09-088, Copyright Permission

Chad:

Authors of published papers in *The Wilson Journal of Ornithology* may use the published paper as part of the degree requirements (i.e., in a Thesis or Dissertation) of a University or College. All that is needed is a statement to the effect the paper (usually a Chapter) is published with the written approval of the Wilson Ornitholigcal Soceity and the paper was published in *The Wilson Journal of Ornithology* 122: 82-87 (2010).

Clait
Clait E. Braun, Ph.D., Editor
The Wilson Journal of Ornithology
Director, Grouse Inc.

AUTHORS' RIGHTS

As a journal author, you retain rights for a large number of author uses, including use by your employing institute or company. These rights are retained and permitted without the need to obtain specific permission from Elsevier. These include:

- the right to make copies (print or electric) of the journal article for their own personal use, including for their own classroom teaching use;
- the right to make copies and distribute copies (including via e-mail) of the journal article to research colleagues, for personal use by such colleagues (but not for Commercial Purposes**, as listed below);
- the right to post a pre-print version of the journal article on Internet web sites including electronic pre-print servers, and to retain indefinitely such version on such servers or sites (see also our information on electronic preprints for a more detailed discussion on these points);
- the right to post a revised personal version of the text of the final journal article (to reflect changes made in the peer review process) on the author's personal or institutional web site or server, incorporating the complete citation and with a link to the Digital Object Identifier (DOI) of the article;
- the right to present the journal article at a meeting or conference and to distribute copies of such paper or article to the delegates attending the meeting;
- for the author's employer, if the journal article is a 'work for hire', made within the scope of the author's employment, the right to use all or part of the information in (any version of) the journal article for other intra-company use (e.g. training), including by posting the article on secure, internal corporate intranets;
- patent and trademark rights and rights to any process or procedure described in the journal article;
- **the right to include the journal article, in full or in part, in a thesis or dissertation;**
- the right to use the journal article or any part thereof in a printed compilation of works of the author, such as collected writings or lecture notes (subsequent to publication of the article in the journal); and
- the right to prepare other derivative works, to extend the journal article into book-length form, or to otherwise re-use portions or excerpts in other works, with full acknowledgement of its original publication in the journal.

Elsevier Global Rights Department
phone (+44) 1865 843 830
fax (+44) 1865 853 333
email: **permissions@elsevier.com**

VITA

CHAD L SEEWAGEN

EDUCATION

PH.D., UNIVERSITY OF WESTERN ONTARIO — LONDON, ON
Received 2010; Major: Biology
Academic advisor: C.G. Guglielmo

M.A., COLUMBIA UNIVERSITY — NEW YORK, NY
Received 2006; Major: Conservation Biology
Academic advisor: C.D. Sheppard

B.S., UNIVERSITY OF MASSACHUSETTS — AMHERST, MA
Received 2002; Major: Wildlife & Fisheries Conservation

WORK EXPERIENCE

11/02 - Present

WILDLIFE CONSERVATION SOCIETY,
BRONX ZOO DEPARTMENT OF ORNITHOLOGY — BRONX, NY
Research Scientist (2009-present); *Project Coordinator* of the New York Bird Monitoring Program (2004-present); *Research Intern* (2002-04)

Field research activities**:**

- Developed urban migratory bird research program in 2004
- Recruit, interview, and hire seasonal field & lab assistants
- Manage field staff of up to nine members at up to five study sites
- Manage annual budgets of $30-70K
- Prepare grant proposals, IACUC protocols, government permit applications
- Coordinate data collection (e.g., study site preparation, mist-netting, blood sampling, bird banding, radio tracking, arthropod sampling); order and maintain equipment/supplies
- Conduct plasma metabolite assays of collected blood samples
- Manage and analyze data; prepare seasonal progress reports and manuscripts for publication in peer-reviewed journals
- Initiate and maintain research collaborations
- Communicate findings to local environmental agencies and land managers
- Organize and conduct educational demonstrations for visiting school groups
- Mentor local high school and graduate students studying birds in NYC; assist with study design, data analyses, and interpretation of findings
- Designed and maintained project webpage (no longer active)

Zoo activities**:**

- Coordinate and advise zoo research interns
- Provide administrative assistance to department curators
- Perform miscellaneous animal keeper duties when assistance needed
- Install exhibit surveillance and nest cameras; edit video footage
- Filmed, edited, produced video ethograms of fairy bluebirds and bee-eater *spp*.

- February-March 2006: Assisted with the establishment of an *in-situ* captive population of hooded pitohuis in Papua New Guinea (captured wild birds, constructed holding cages, established temporary husbandry protocol)

6/05 - Present WILDLIFE CONSERVATION SOCIETY, NORTH AMERICA PROGRAM SARANAC LAKE, NY
Field Ornithologist, Adirondack Mountains

- 2005-Present: Conduct surveys of Bicknell's thrush and other boreal breeding bird species to assess impacts of ski trail development
- 2006: Conducted rapid assessments of breeding bird diversity on paper company properties to evaluate forestry practices; prepared summary of findings

1/06 - Present PHILADELPHIA ZOO PHILADELPHIA, PA
Research Consultant

- Consulted on the design and implementation of an urban stopover ecology research project in Philadelphia
- Analyze the project's seasonal bird banding data; prepare summaries of findings

7/07 - 9/07 NEW YORK CITY AUDUBON NEW YORK, NY
Consultant

- Reviewed and synthesized literature on bird collisions with windows as an annotated bibliography

5/02 - 9/02 VERMONT DEPARTMENT OF FISH AND WILDLIFE SPRINGFIELD, VT
Seasonal Fisheries Technician

- Conducted river habitat surveys (widths, depths, temps, cataloguing of coarse woody debris, tributary mapping)
- Sampled Atlantic salmon, trout, and bass by electro-fishing
- Monitored fish migration along the Vernon Dam fish ladder

6/99 - 8/99 USGS ANADROMOUS FISH RESEARCH CENTER TURNER'S FALLS, MA
Seasonal Fisheries Technician

- Sampled Atlantic salmon by electro-fishing and night-seining
- Implanted PIT-tags into juvenile Atlantic salmon

TEACHING EXPERIENCE

2007-2010 UNIVERSITY OF WESTERN ONTARIO LONDON, ON
Teaching Assistant

- "Animal Ecology": Led field trips on which undergraduate students learned about winter weeds, goldenrod and gallfly ecology, and habitat restoration. Led lab sessions in which students learned common field sampling techniques, statistical analyses, and how to write scientific proposals and papers. Graded research proposals and reports.

- "Analysis and Interpretation of Biological Data": Led computer lab sessions in which undergraduates completed exercises in univariate statistical analyses using SPSS. Graded bi-weekly assignments.

- "Introduction to Biology": Led lab sessions in which undergraduate students conducted various cellular and molecular biology experiments. Graded bi-weekly assignments.

8/06 NEW YORK CITY BOARD OF EDUCATION BRONX, NY
Teacher Training Consultant
- Coordinated professional development workshop in which elementary school science teachers learned how to implement lessons about bird behavior, migration, and conservation in their classrooms. Demonstrated basic research field techniques.

VOLUNTEER SERVICE

5/09 - Present BIRD-SAFE GLASS FOUNDATION NEW YORK, NY
Scientific Advisory Board member
- Attend monthly board meetings to discuss strategies for reducing bird mortality caused by building and window collisions.

6/04 - 1/09 BRONX RIVER ALLIANCE BRONX, NY
Ecology Team member
- Attended monthly meetings; advised watershed habitat restoration and management strategies.
- Reviewed and wrote contributions for the *State of the River* report.

10/02, 9/04, 10/06, 10/09 CAPE MAY RAPTOR BANDING PROJECT CAPE MAY, NJ
Volunteer Banding Assistant
- Trapped and banded birds of prey using bow-, mist-, and Dho-gaza-nets

GRANTS & AWARDS

- New York City Audubon. $1,350 received Apr. 2009
- Black Rock Forest Consortium. $5,000 received Feb. 2009 (Co-PI)
- Eastern Bird Banding Association. $1,000 received March 2009 (Co-PI)
- New York City Audubon. $3,500 received Oct. 2008
- New York State Department of Environmental Conservation, Environmental Benefit Project. $150,000 received Feb. 2008
- McKenzie River Gathering Foundation. $1,000 received Feb. 2008
- The Moore Charitable Foundation. $4,500 received Aug. 2007
- Westchester Department of Parks and Recreation. In-kind contributions (field staff salaries and housing) 2007-09 valued at approximately $10,000.
- Wildlife Conservation Society, Conservation Award. $15,000 received Feb. 2007
- University of Western Ontario, Graduate Research Scholarship. $40,000 awarded Jun. 2006
- University of Western Ontario, Graduate Research Scholarship Bonus for securing external awards. $16,000 awarded Jun. 2006
- Wildlife Conservation Society, Species Survival Fund. $2,500 received Sep. 2005
- Nuttall Ornithological Club, Charles Blake Fund. $2,000 received Oct. 2005
- Wildlife Conservation Society, Species Survival Fund. $5,000 received Sep. 2004

PUBLICATIONS

- **Seewagen, C.L.**, E.J. Slayton, C.D. Sheppard, and C.G. Guglielmo. *In Review*. Plasma metabolites and mass changes of migratory landbirds indicate adequate stopover refueling conditions are available in a heavily urbanized landscape. *The Condor*.

- Snyder, B.A. and **C.L. Seewagen**. *In Press*. First record of the millipede *Cleidogona nantahala* (Chordeumatida: Cleidogonidae) for New York State. *Entomological News*.

- **Seewagen, C.L.** and C.G. Guglielmo. *In Press*. Quantitative magnetic resonance analysis and a morphometric model reveal lean body mass changes in migrating Nearctic-Neotropical passerines. *Journal of Comparative Physiology B*.

- Thomas, R.H., E.R. Price, **C.L. Seewagen**, S.A. MacKenzie, M.A. Bernards, C.G. Guglielmo. 2010. Use of TLC-FID and GC-MS/FID to examine the effects of migratory state, diet, and captivity on preen wax composition of White-throated Sparrows. *Ibis* 152(4):782-792.

- **Seewagen, C.L**., E.J. Slayton, and C.G. Guglielmo. 2010. Passerine migrant stopover duration and spatial behaviour at an urban stopover site. *Acta Oecologica* 36(5):484-492.

- **Seewagen, C.L**. and C.G. Guglielmo. 2010. Effects of fat and lean body mass on migratory landbird stopover duration. *Wilson Journal of Ornithology* 122(1):82-87.

- **Seewagen, C.L.** 2010. Threats of environmental mercury to birds: knowledge gaps and priorities for future research. *Bird Conservation International* 20(2):112-123.

- **Seewagen, C.L.** and E.J. Slayton. 2008. Mass changes of migratory landbirds during stopovers in a New York City park. *Wilson Journal of Ornithology* 120(2):296-303.

- **Seewagen, C.L.** 2008. An evaluation of condition indices and predictive models for non-invasive estimates of lipid mass of migrating Common Yellowthroats, Ovenbirds, and Swainson's Thrushes. *Journal of Field Ornithology* 79(1):80-86.

- **Seewagen, C.L.** 2008. Bird collisions with windows: an annotated bibliography. New York City Audubon, New York, USA. 15pp.

- **Seewagen, C.L.** 2008. Lipid content of Nearctic-Neotropical migratory passerines killed during stopovers in a New York City park . *Northeastern Naturalist* 15(1):87-96.

- **Seewagen, C.L.** and E.J. Slayton. 2006. Historical accounts of Bicknell's Thrush in New York City and a new record for Bronx County. *Kingbird* 56(3):210-215.

PEER REVIEWS

- Peer reviewer for *Journal of Avian Biology, Journal of Field Ornithology, Wilson Journal of Ornithology*.

- Editorial Board member for *The Kingbird*, a peer-reviewed, quarterly journal of the New York State Ornithological Association.

PRESENTATIONS

- **Seewagen, C.L.** and C.G. Guglielmo. Ovenbird spatial behavior at an urban stopover site: movement patterns, stopover durations, and the influence of arrival condition. Presented at:
  −Annual meeting of the Wilson Ornithological Society, May 2010, Geneva, NY.

- **Seewagen, C.L.** and C.G. Guglielmo. Can urban parks provide suitable stopover habitat for migratory landbirds? A call for additional research. Presented at:
  −International Symposium on Urban Wildlife Ecology & Management, Jun. 2009, Amherst, MA.

- **Seewagen, C.L.** and E.J. Slayton. Stopover ecology of Neotropical migratory birds in an urban park. Presented at:
  −North American Ornithological Conference, Oct. 2006, Veracruz, Mexico.
  −Annual meeting of the New York State Ornithological Association, Oct. 2006, Oneonta, NY.
  − Conserving Birds in Human Dominated Landscapes, American Museum of Natural History, Apr. 2006, New York, NY. (Poster)
  −Northeast Natural History Conference IX, New York State Museum, Apr. 2006, Albany, NY. (Poster).

- **Seewagen, C.L**. The role of urban habitats as stopover sites for migratory birds. Presented at:
  −Great South Bay Audubon Society, Nov. 2008, Oakdale, NY.
  −Greenwich Audubon Society, Sep. 2006, Greenwich, CT.
  −Annual meeting of the Catskill Bird Club, Jul. 2006, Monticello, NY.
  −Annual meeting of the Eastern Bird Banding Association, Mar. 2006, Bethlehem, PA.

- Guglielmo, C.G., A. Gerson, L. McGuire, **C.L. Seewagen**. Rapid, non-invasive and direct measurement of fat mass, lean mass, and body water of wild birds using a field-portable magnetic resonance scanner. Presented at:
  −Annual meeting of the American Ornithologists' Union, Aug. 2008, Portland, OR. (Poster).

- Guglielmo, C.G., L. McGuire, A. Gerson, **C.L. Seewagen.** Quantitative nuclear magnetic resonance to measure body composition of bats and birds. Presented at:
  −First International Symposium on Bat Migration, Jan. 2009, Berlin, Germany.

CURRENT RESEARCH

- **Seewagen, C.**, D. Evers, and C. Guglielmo. Intra-individual measures of mercury and stopover refueling performance in the Northern waterthrush.
- DeCandido, R., D. Allen, **C. Seewagen**. Nest-site selection of American kestrels in New York City.
- **Seewagen, C**., D. Allen, K. Bildstein, D. Cristol, R. DeCandido, R. Horvath, J. Smallwood. Mercury and lead levels of American kestrels along an urban-rural gradient.
- Gillett, A. and **C. Seewagen**. Effects of mercury on red-winged blackbird nestling development in the New York metropolitan area.
- Glennon, M., L. Karasin, **C. Seewagen**. Effects of ski trail development on the threatened Bicknell's thrush and other high-elevation breeding birds on Whiteface Mountain, New York.
- Guglielmo, C.G., A. Gerson, L. McGuire, **C. Seewagen.** A validation of quantitative magnetic resonance analysis for non-invasive measurement of the body composition of birds.
- **Seewagen, C.**, D. McGovern, V. Peckham, K. Russell. Mass change rates of migratory songbirds at a Philadelphia stopover site.

PRESS COVERAGE

- Mahony, M. Taverns in the green. *Wildlife Conservation*, Mar. 2008.
- Lloyd, R. Migrating birds bulk up in the Big Apple. *LiveScience.com*., 2007.
- Berreby, D. A bird's life. *The New Yorker*, Nov., 2007.
- Shalant, J. The perils and perks of migration. *Wildlife Conservation*, Feb. 2007.
- Appleton, A. The songbird and the city. *Columbia Science Review*, Spring 2006.
- Gill, J. Keeping tabs on feathered waistlines. *The New York Times*, May 8, 2005.

PROFESSIONAL MEMBERSHIPS

- American Ornithologist's Union
- Association of Field Ornithologists
- New York State Ornithological Association
- Wilson Ornithological Society

COMPUTER SKILLS

- SYSTAT, SPSS, and Prism statistical analysis packages
- Hawth's Tools and Animal Movement extensions for ArcGIS
- Raven Pro animal sound analysis software
- Adobe Premiere Pro real-time video editing software

LICENSES & CERTIFICATIONS

- NAUI Advanced Scuba Diver
- New York State driver's license